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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

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ISSN 0706-652X / CJFSDX 61(2) 147–322 (2004)

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Volume 61, Number 2, February 2004

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 61, numéro 2, février 2004

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Publié par le Conseil national de recherches du Canada

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Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada

Alexandra Morton, Richard Routledge, Corey Peet, and Aleria Ladwig

Abstract: This study compared sea lice (*Lepeophtheirus salmonis*) infestation rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in five nearshore areas of the British Columbia coast selected on the basis of proximity to salmon farms. A 10-week study in the Broughton Archipelago found sea lice were 8.8 times more abundant on wild fish near farms holding adult salmon and 5.0 times more abundant on wild fish near farms holding smolts than in areas distant from salmon farms. We found that 90% of juvenile pink and chum salmon sampled near salmon farms in the Broughton Archipelago were infected with more than 1.6 lice·(g host mass)$^{-1}$, a proposed lethal limit when the lice reach mobile stages. Sea lice abundance was near zero in all areas without salmon farms. Salinity and temperature differences could not account for the higher infestation rates near the fish farms. The most immature life stages dominated the lice population throughout the study, suggesting the source of lice was a stationary, local salmonid population. No such wild population could be identified. The evidence from this control–impact study points to a relationship between salmon farms and sea lice on adjacent, wild, juvenile salmon.

Résumé : Notre étude compare les taux d'infestation des poux de mer (Lepeophtheirus salmonis) chez le saumon rose (Oncorhynchus gorbuscha) et le saumon kéta (Oncorhynchus keta) dans cinq régions côtières de la Colombie-Britannique, choisies à cause de la proximité d'élevages de saumons. Une recherche de 10 semaines dans l'archipel de Broughton révèle que les poux de mer sont 8,8 fois plus abondants chez les poissons sauvages à proximité d'élevages contenant des saumons adultes et 5,0 fois plus abondants aux environs d'élevages contenant des saumoneaux que dans les zones situées loin des élevages de saumons. Quatre-vingt-dix pour cent des jeunes saumons roses et kéta échantillonnés près des élevages de saumon dans l'archipel de Broughton portent des infestations supérieures à 1,6 pou·(g de masse de l'hôte)$^{-1}$, une limite que nous considérons létale lorsque les poux atteignent les stades mobiles. Les densités de poux de mer sont presque nulles dans toutes les régions sans élevage de saumons. Les différences de salinité et de température n'expliquent pas les taux plus élevés d'infestation à proximité des élevages. Ce sont les stades les plus immatures qui dominent dans la population au cours de l'étude, ce qui laisse croire que la source des poux est une population locale et stationnaire de salmonidés. Nous n'avons trouvé aucune population sauvage qui possède de telles caractéristiques. Les données de notre étude de type témoin–impact indiquent qu'il existe une relation entre les élevages de saumon et les poux de mer qui parasitent les jeunes saumons sauvages des régions adjacentes.

[Traduit par la Rédaction]

Introduction

The sea louse *Lepeophtheirus salmonis* is a common salmonid-specific caligid ectoparasite in the Northern Hemisphere. Salmon examined on the high seas are commonly infected with low numbers of adult *L. salmonis* (Nagasawa et al. 1993). Pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon 20–79 cm (fork length) were the most heavily infected; 91.8% prevalence and 5.83 lice·fish^{-1} mean intensity for pink salmon and 15.9% prevalence and 2.28 lice·fish^{-1} mean intensity for chum salmon (Nagasawa 1987; Nagasawa et al. 1993). The scarcity of im-

Received 12 April 2003. Accepted 24 January 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 2 March 2004.
J17463

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 doi: 10.1139/F04-016 © 2004 NRC Canada

mature lice on salmon at sea contrasts with the predominantly juvenile lice populations found exclusively on hosts in nearshore, salmon-farmed areas of Ireland and Norway (Tully et al. 1993; Bjørn and Finstad 2002) and is considered evidence of infrequent infection events at sea (Pike and Wadsworth 1999).

Reported epizootics of *L. salmonis* were rare, although noted (White 1940), until acute sea lice infestations were reported on farmed salmon in Norway (Håstein and Bergsjo 1976) and Scotland (Wootten et al. 1982; Stuart 1990). Following these reports, high infestation rates were recorded in wild salmonids near salmon farms in Ireland and Norway (Tully et al. 1993; Birkeland 1996). Today, sea lice epizootics have been reported in most areas where there are large numbers of salmon farms (Anonymous 1997). It is generally accepted that sea lice infestations on farmed salmonids are caused by transfer from wild stocks, because farm salmon enter the marine environment lice free. However, vigorous debate is underway over whether the farms' stationary, high-density host populations in the nearshore marine environment act as a sea lice reservoir capable of reversing the transmission to juvenile wild stocks out-migrating through the zone of influence of farm-origin lice larvae.

Lepeophtheirus salmonis has a direct life cycle of five discrete phases and 10 stages (Johnson and Albright 1991*a*) that allows the approximate age of individual sea lice to be determined. This is useful in interpreting infective events as discrete or continuous and local or distant. The ability of sea lice to find a host is limited by time and therefore distance. The eggs hatch from gravid females into free-swimming nauplii (Kabata 1972). The interval between hatching (the naupliar stages) and infective capability (the copepodid stage) is approximately 4 days at 10 °C and 2 days at 15 °C (Johnson and Albright 1991*b*). The free-swimming, infective copepodid stage, during which host attachment must occur or the parasite dies, lasts for 2–8 days at 5–15 °C (Wootten et al. 1982; Johnson and Albright 1991*b*). Larval lice, which exhibit phototaxis (Johannessen 1978), disperse via oceanic surface currents (Anonymous 1995) and decline in numbers as distance increases from salmon farms (Costelloe et al. 1996).

Once attached to a host, *L. salmonis* remains anchored in one location as it moults through four chalimus stages. Upon entering the next, pre-adult phase, sea lice become mobile (Johnson and Albright 1991*a*), and this transition marks the onset of host pathogenicity (Grimnes and Jakobsen 1996). Studies on European salmonids (Arctic char (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*), and sea trout (*Salmo trutta*)) suggest that the lethal infection level of post-smolts is between 0.75 and 1.6 mobile lice·(g host mass)$^{-1}$, mean mass 60–90 g (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997).

A recent series of events on the central coast of British Columbia (B.C.), Canada, bear similarity to European collapses of wild stocks infected with sea lice near salmon farms and served as the impetus for this study. There are 28 Atlantic salmon farm tenures in the Broughton Archipelago. In 2000, there was an exceptionally high spawning escapement of pink salmon into the rivers of the Broughton Archipelago (PFRCC (Pacific Fisheries Resource Conservation Council) 2002), in addition to a commercial catch of 2×10^6 of this stock (Glen Neidrauer, Department of Fisheries and Oceans Patrolman, Simoom Sound, BC V0P 1S0, Canada, personal communication). In June 2001, Morton and Williams (2004) examined the progeny of this stock to record the first known incidence of *L. salmonis* infestation of juvenile pink salmon. Seventy-five percent (mean host mass 2.26 g) were infected with 1.6 lice·(g host mass)$^{-1}$ or more. When this generation returned to spawn, a 98% spawning escapement collapse, specific only to the rivers in the Broughton Archipelago, was reported (PFRCC 2002). The PFRCC (2002) suggested "causal factors should be sought in the nearshore environment" because no causative freshwater factors could be identified, and the spatial range of this collapse was so localized. While density-dependent effects in the nearshore environment may have contributed to the population decline, the magnitude of reduction between progeny and parental line is well outside the natural high survival variability recorded for this species over the past 50 years (PFRCC 2002).

Pink and chum salmon biology is significantly distinctive among salmonids because they do not rear in fresh water, and this may be a critical factor when attempting to quantify the magnitude of impact by sea lice. Pink salmon enter the marine environment at 3.5 cm (Heard 1991) and chum salmon enter at 4.0 cm (Bax 1983). These are four to five times smaller than the Atlantic salmonids (Scott and Crossman 1973). Because sea lice impact is host size dependent (i.e., the smaller the fish, the fewer lice required to induce negative effects) (Bjørn and Finstad 1997), it is possible that pink and chum salmon may be more sensitive to sea lice infection than the larger juvenile salmonid species found in Europe. Pink salmon have a fixed 2-year cycle (Heard 1991), while chum salmon in B.C. return at 3, 4, and 5 years old (Salo 1991).

Sea lice infestation intensities show considerable geographic and temporal variability (Boxaspen 1997). To date, no studies have been conducted in B.C. to examine the variability of louse infection intensities across a geographic range.

The object of this study was to compare sea lice infestation rates on wild out-migrating juvenile salmon at locations near to and distant from salmon farms and over time. This was done both within the Broughton Archipelago and less intensively at intervals to the north, well beyond the range of larval lice produced from any salmon farm. We compared the incidence, age, and species of sea lice populations found on juvenile pink and chum salmon among regions of coastal B.C. waters and variation with respect to proximity to salmon farms.

Methods

Juvenile pink and (or) chum salmon were sampled from five areas of the B.C. coast in the spring of 2002 (Fig. 1). In the Broughton Archipelago, up to 20 juvenile pink and (or) chum salmon were collected once a week for 10 weeks from six sites and twice only from an additional site beginning on 16 April for a total of 1072 fish. A dip net (45 cm diameter of 5-mm knotless mesh) on a 2.45-m pole (Bailey et al. 1975) was used for collection. Sites 1, 2, and 3 were control sites: distant from salmon farms but comparable (possessed similar physical and oceanographic conditions) with the ex-

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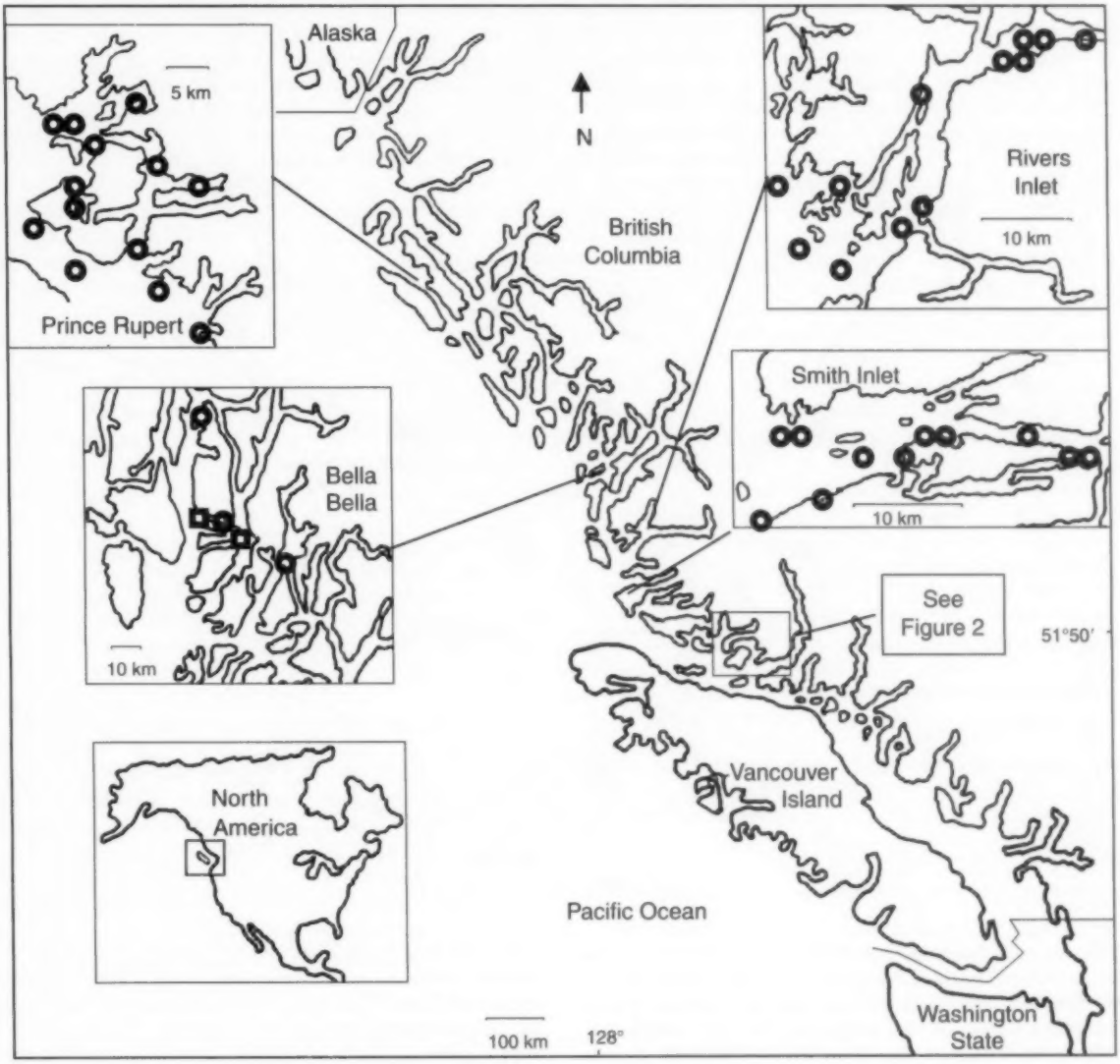
Fig. 1. Map of the coast of British Columbia, Canada, showing all five areas where juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon were sampled and the location of the general area within North America. Collection sites are indicated by a circle, and salmon farms outside the Broughton Archipelago are indicated by a square.



posed categories (smolt and grower) except for proximity to farms. No samples were taken, for example, from brackish water; salinity levels remained above 12‰. Sites 4, 5, and 6 were within 250 m of an active Atlantic salmon farm stocked with growers (i.e., fish in their second year in seawater). Site 7 was within 250 m of a farm stocked with smolts (i.e., salmon in their first year in salt water) and was only sampled twice (Fig. 2).

Seventy-five kilometres to the north, 48 juvenile pink salmon were collected on 6 June and 3 July from 11 sites in Smith Inlet. Ninety kilometres north of the Broughton Archipelago, 250 juvenile pink salmon were collected on 10 dates from 13 May through 4 July from 12 sites in Rivers Inlet (Fig. 1). At both of these sites, a 300-m-long purse seine, 30 m deep with 6-mm mesh, was deployed close to shore from a 15-m seine boat. The net was held in the water and the fish removed individually with a dip net fitted with knotless Marquisette mesh to minimize scale and lice loss.

One hundred eighty kilometres north of the Broughton Archipelago, 154 juvenile pink and chum salmon were collected from three nearshore sites on 27 June through 2 July in the Bella Bella area (Fig. 1) using a dip net (45 cm diameter with 5-mm mesh) on a 2.45-m pole from a shallow draft 4-m boat. As the juvenile salmon out-migration season was nearly completed, sites were selected based on the availability of out-migrating smolts using the following criteria: at least 1 km away from a major freshwater source and close to shore. A maximum of 60 fish were collected from each site.

Four hundred kilometres north of the Broughton Archipelago off Prince Rupert, 566 pink and chum salmon were col-

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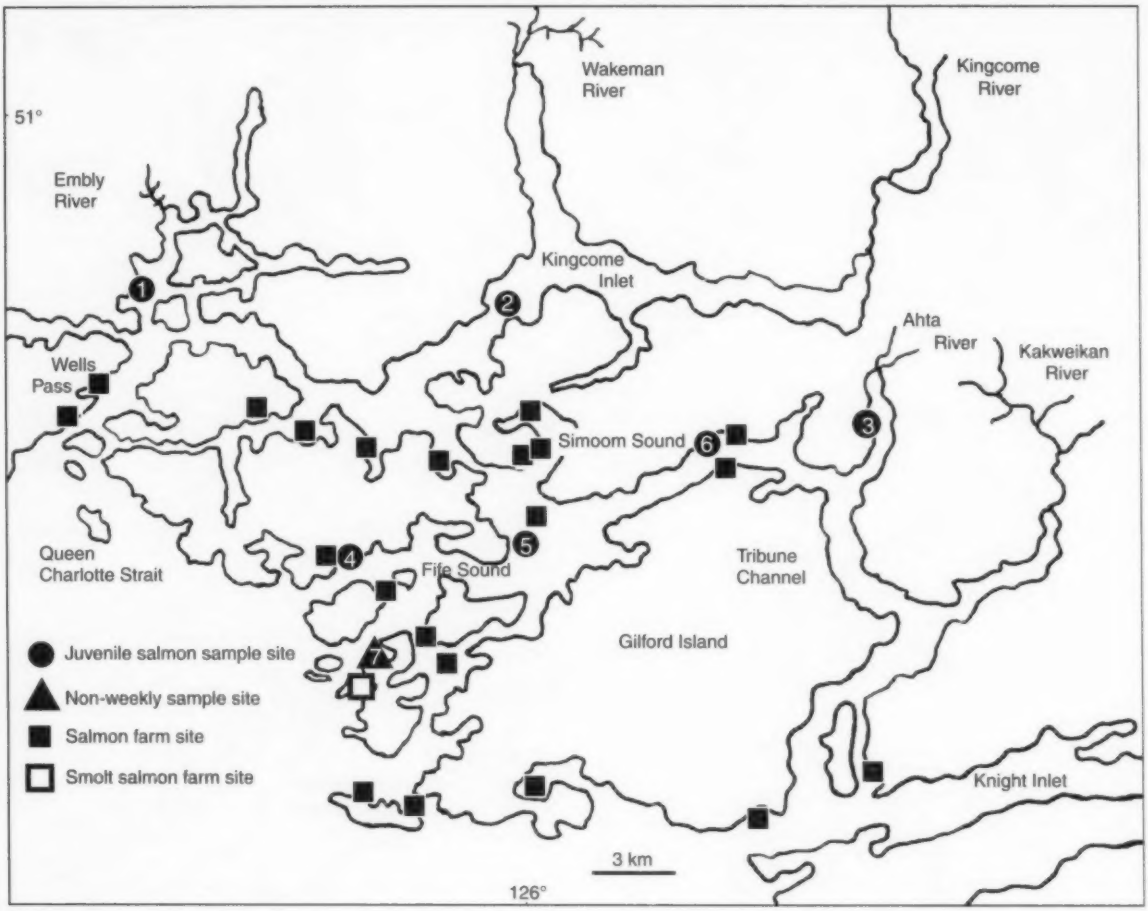
Fig. 2. Map of the seven sites sampled in the Broughton Archipelago over the 10-week period. Sites 1, 2, and 3 were control sites (distant from salmon farms); sites 4, 5, and 6 were exposed to salmon farms stocked with growers (second year in salt water); and site 7 was exposed to a farm stocked with smolts (first year in salt water) and was only sampled twice during the study.



lected using a 30.5-m-long, 2-m-deep beach seine with 0.3-cm mesh in the bunt and 0.6-cm mesh on the wings and a 13-cm-diameter dip net on a 31-cm pole on 11 dates from 6 May through 2 June from 13 sites (Fig. 1). Over 400 km of shoreline was surveyed and up to 25 juvenile pink and or chum salmon collected at each site where fish were encountered.

At all sites, other than Rivers Inlet and Smith Inlet, fish were placed individually in Whirlpak™ bags immediately after capture, placed on ice, and frozen shortly thereafter. At Rivers Inlet and Smith Inlet, samples were preserved in ethanol in jars. Later, fish were weighed, measured (fork length), and the number and species of sea lice recorded using a × 30 magnification stereoscope.

Sea lice were categorized by species, sex, and life history stage (Johnson and Albright 1991*a*). *Caligus* and *Lepeophtheirus* chalimus stage lice were distinguished from each other using Piasecki (1996) and Johnson and Albright (1991*a*).

The measures of lice infestation rates are defined as follows. Prevalence, usually expressed as a percentage, is the number of individual hosts infected with lice. Intensity is the number of lice on each infected host. Abundance is the total number of lice divided by the total number of hosts (infected and uninfected) (Margolis et al. 1982).

The null hypothesis of primary concern was that the average abundance of sea lice did not depend on proximity of a sampling site to a fish farm or on its geographic area. Choosing the appropriate statistical method to test that hypothesis was a complex task. The analysis also had to account for (and assess) possible differences over time and potential confounding effects that are unavoidably present in any control–impact study. Here, salinity and temperature were of primary concern. Potential differences between host species (pink vs. chum salmon) also needed to be included in the analysis. Furthermore, with count data, the variance usually increases with the mean. Hence, the analysis had to be able to handle multiple factors, some categorical (e.g., geographic area) and others continuous (e.g., salinity and temperature), and to handle heteroscedasticity. In addition, so that inferences on the impacts of other factors would not be limited to the particular sites sampled, these had to be

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viewed as random. This also implied that any site–week interactions be treated as random.

Where appropriate, we chose the now standard method of loglinear modeling for handling count data with mixed (fixed and random) effects (McCulloch and Searle 2001), analyzed using the SAS macro, GLIMMIX. The response variable was the number of lice per fish. For *L. salmonis*, we were able to simplify the analysis by focusing on the Broughton Archipelago, the only area with significant louse abundance. We first fit a full model with all potentially relevant factors as listed above. Then for subsequent analyses, we dropped those factors that were not significant at the conventional level $p = 0.05$. The tests were conducted by examining the ability of each variable in turn to explain further variation in the data with each of the other variables in the model. The p value for salinity, for example, assessed the existence of any remaining relationship between salinity and lice abundance after the influence of all other factors was accounted for. The reasoning is analogous to that used in multiple regression modeling (Kleinbaum et al. 1998). We also calculated denominator degrees of freedom with a Satterthwaite approximation (using the SAS option, ddfm = satterth). The resulting degrees of freedom were not always whole numbers.

We checked for autocorrelation between successive weeks at a single site (positive autocorrelation being of particular concern in that it could lead to inflated significance). Since the lag-1 autocorrelation estimate was not even positive ($r = -0.21$) and not statistically significant ($t = -1.77$, $p = 0.084$), autocorrelation was not included in any of the subsequent statistical analyses.

Multiple comparisons were made with conservative adjustments for the number of comparisons based on Bonferroni's inequality (Miller 1981). The experiment-wise significance level for these tests was set to 5%. These analyses were then repeated for *L. salmonis* adults and then again for juveniles. For the adults, however, there were very low abundances (lice per fish) at the start of the sampling period. Although this is a valuable observation, it created a situation where the nonzero counts were too sparse for us to trust the theoretical approximations underlying the GLIMMIX algorithms and output. We therefore chose to analyze these counts with the more traditional (e.g., Steel and Torrie 1980) yet conceptually similar expedient of transforming the counts (y) to $\log_e(y + 0.5)$ and then applying a linear model. Because sites were still to be viewed as random, we used the SAS procedure MIXED for this analysis.

The *Caligus* counts were, by contrast, not restricted so intensively to the Broughton Archipelago, nor were they anywhere as abundant. Hence, we were again faced with sparse nonzero counts. To promote the accuracy of the theoretical approximations, we made two alterations to the modeling strategy. We performed the more traditional analysis described above, with a further a priori exclusion of all but the essential terms in the model for testing for differences in mean abundances among exposure categories and geographic areas. The exclusion of these other terms, while necessary to promote the validity of the theoretical approximations, will have potentially inflated the amount of unexplained variation. This in turn will have made it more difficult to detect the influence of the remaining factors in the model. Hence, the resulting tests of significance should be viewed as conservative.

As there were no funds dedicated solely to this study, we opportunistically shared juvenile salmon sampled by other research projects outside the Broughton Archipelago. While this allowed for a quick response to the question "How do lice loads on juvenile Pacific salmonids compare coastwide?", it meant we did not control collection methods. Each method used in this study has advantages and each introduces a form of bias.

Dip-netting subjects fish to the minimum duration in a net and therefore may be least likely to remove lice or scales. Dip nets successfully capture juvenile pink salmon because at this life stage, these fish typically remain in shallow water (Healey 1980) where they occupy only the top few centimetres of the water column (Parker 1965). As chum salmon were equally abundant in our samples, they appeared to behave similarly, at least while schooled with pink salmon.

Dip-netting could select for weaker fish; however, any such sampling bias would have been consistent over all sites throughout the 10 weeks of the Broughton study, the Bella Bella samples, and most of the Prince Rupert samples.

The seine net used in Smith and Rivers inlets could remove scales and lice if hauled aboard, but the net was held in the water against the boat and the fish removed individually with a knotless mesh dip net. The seine also introduces unknown potential for selectivity that differs from the dip net. Once the fish were trapped in the bunt, there was no escape, but before that time escape was possible, particularly on sets where tidal turbulence, gusty winds, etc., caused difficulties, and some fish almost surely did escape. However, one would anticipate that the vigorous fish would be most likely to escape and that the more sluggish, lice-infested fish would be more likely to be caught. Hence, sampling bias appears not to be a reasonable explanation for the near-zero lice infestation rates in these samples.

Results

We collected a total of 2090 fish and all were examined for lice. The mean fork lengths and masses were smallest in Bella Bella, nearly identical between Prince Rupert and the Broughton Archipelago, and largest in Rivers and Smith inlets (Table 1). The average mass of the pink and chum salmon we captured in the first 3 weeks in the Broughton Archipelago was 0.33 g. Mean salinity values were recorded (Table 1). Average temperature for the Broughton Archipelago was 10.4 °C.

Lepeophtheirus salmonis was rare in our samples outside the Broughton Archipelago: three lice total on 1018 juvenile pink and chum salmon (Fig. 3, Table 2). By contrast, 4338 *L. salmonis* individuals were found on 1138 juvenile pink and chum salmon sampled from the Broughton Archipelago (an additional 364 lice were *Caligus*). Over the 10-week study period, the overall abundance of *L. salmonis* increased to a peak in week 9 (Fig. 4).

The abundance of *L. salmonis* was much higher on fish sampled at grower sites than on those at control sites, with an intermediate abundance at the smolt site (Fig. 5, Table 2). Overall (grower, smolt, and controls sites), we found 90% of pink and chum salmon to be infected at or above what could

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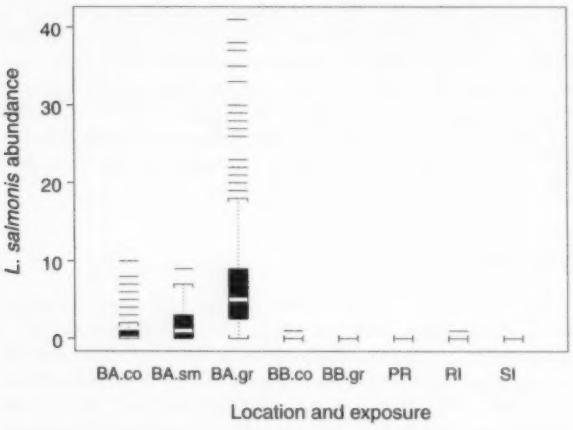
Table 1. Mean fork length (cm) and mass (g) of juvenile salmon and salinity (‰) per location and exposure.

Location	Fork length (SE)*	Mass (SE)*	Exposure	Salinity
Prince Rupert	4.44 (0.05)	1.02 (0.05)	—	33.6
Bella Bella	3.76 (0.06)	0.63 (0.05)	Grower	21.0
			Control	11.9
Rivers Inlet	7.78 (0.09)	3.97 (0.12)	—	1.3–14.0
Smith Inlet	7.59 (0.20)	3.82 (0.32)	—	23.0
Broughton Archipelago	4.45 (0.04)	1.07 (0.04)	Grower	28.6
			Control	23.2

*Standard error is given in parentheses.

Fig. 3. Presentation of abundance of sea lice (*Lepeophtheirus salmonis*) on juvenile salmon sampled in all five areas for exposure categories. In each instance, the darkened box represents the middle half of the values (between the lower and upper quartiles). The lighter line inside this box is at the median. The whiskers extend beyond each quartile by 1.5 times the interquartile range (the height of the box). Isolated bars beyond these whiskers designate individual values beyond these limits (outliers). BA.co, Broughton Archipelago control (distant from salmon farm); BA.sm, Broughton Archipelago smolt site; BA.gr, Broughton Archipelago grower sites; BB.co, Bella Bella control (distant from salmon farms); BB.gr, Bella Bella grower sites; PR, Prince Rupert (no salmon farms in region); RI, Rivers Inlet (no salmon farm in region); SI, Smith Inlet (no salmon farm in region).



become the lethal limit when and if the lice reach a mobile stage (1.6 mobile lice·(g host mass)$^{-1}$), as described by Bjørn and Finstad (1997) for sea trout. The mean number of sea lice on salmon near salmon farms was 6.99, while the mean mass of the pink and chum salmon was 1.07 g. As outlined below, infestation was not significantly different between pink salmon and chum salmon ($p = 0.89$) (Fig. 6, Table 3).

The *L. salmonis* counts were fit with a generalized linear mixed model to test for the influence of the following factors: salinity, temperature, host species, week, and exposure category. Also, to allow for different time dependence for different exposure categories, we included the interaction of the last two factors. In addition, location (nested within exposure category) was added as a random factor to allow inferences to extend beyond these particular locations. We used this analysis to test the null hypotheses that each of these factors had no influence on abundance (results are summarized in Table 4). Of the fixed factors in this model, only exposure category ($p = 0.027$), week ($p < 0.0001$), and their interaction ($p = 0.013$) were significant. A more parsimonious model excluding the nonsignificant factors (temperature, salinity, and host species) was then fit. This model generated the same main conclusions: (*i*) differences in lice levels between exposure categories could not be attributed to chance ($p = 0.001$), (*ii*) lice levels also changed significantly over time ($p < 0.0001$), and (*iii*) this time behaviour depended on the exposure category ($p = 0.009$). Furthermore, the coefficients in this model can be used to estimate that mean lice infestation rates, after accounting for effects of other uncontrolled but influential factors, were about eight times higher in those sites impacted by grower farms vs. the control sites.

When the counts of juvenile *L. salmonis* were analyzed separately, the same effects remained significant. However, in the parsimonious model for adult *L. salmonis*, the only significant factor was time. Thus, the time fluctuations in Fig. 7 are not attributable to chance fluctuations, and exposure status has a significant impact on juvenile lice abundance but not on adult lice abundance. Note also the sustained presence of the copepodid stage and a roughly exponential growth of adult lice up to week 9 of this study in the Broughton Archipelago (Fig. 7).

A sample of *Caligus* from this study was identified as *Caligus clemensi* (P.A. Heuch, National Veterinary Institute, P.O. Box 8156, Dep., N-0033 Oslo, Norway, personal communication). These lice were more dispersed, with particularly substantial numbers found in the sites exposed to salmon farms near Bella Bella (Fig. 8). They were also nowhere as abundant as *L. salmonis* were in the Broughton Archipelago. These smaller numbers and the geographic dispersion ruled out not only the generalized linear modeling approach, but also a more geographically focused and complex analysis of the abundance patterns. We therefore included in the statistical model terms only for (*i*) fixed effects for area and exposure status and (*ii*) random effects for sites. The exclusion of other terms will likely have led to the overestimation of the degree of chance variation in the random site effects, and hence the production of conservative (larger) *p* values. We tested the null hypotheses that area and expo-

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Table 2. Mean abundance of lice per fish for all areas and exposure categories moving from the most southerly site to the most northerly.

		Lepeophtheirus salmonis				*Caligus* spp.			
Area	No. of fish sampled	Total	Mean abundance	SD	SE of mean	Total	Mean abundance	SD	SE of mean
Broughton									
Control	537	437	0.814	1.356	0.059	21	0.039	0.329	0.014
Smolt	37	79	2.135	2.371	0.390	79	2.135	3.591	0.590
Grower	564	3822	6.777	6.361	0.268	264	0.468	2.308	0.097
Smith Inlet	48	0	0.000	0.000	0.000	0	0.000	0.000	0.000
Rivers Inlet	250	0	0.000	0.000	0.000	1	0.004	0.063	0.004
Bella Bella									
Control	118	1	0.008	0.092	0.008	1	0.008	0.092	0.008
Grower	36	0	0.000	0.000	0.000	28	0.778	1.072	0.179
Prince Rupert	566	2	0.004	0.059	0.002	4	0.007	0.084	0.004

Note: SD, standard deviation; SE, standard error.

Fig. 4. Weekly abundance of sea lice (*Lepeophtheirus salmonis*) on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the Broughton Archipelago over 10 weeks. See Fig. 3 for interpretation of box plots.

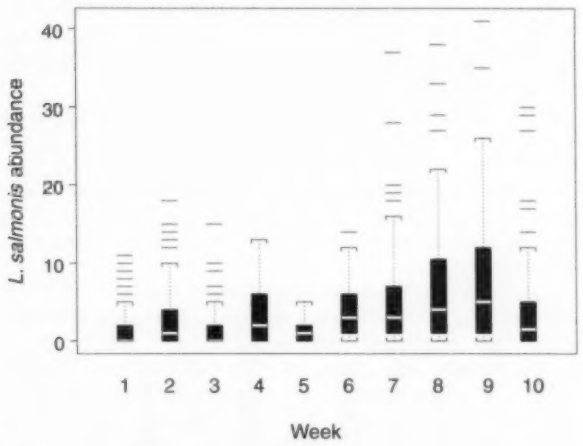
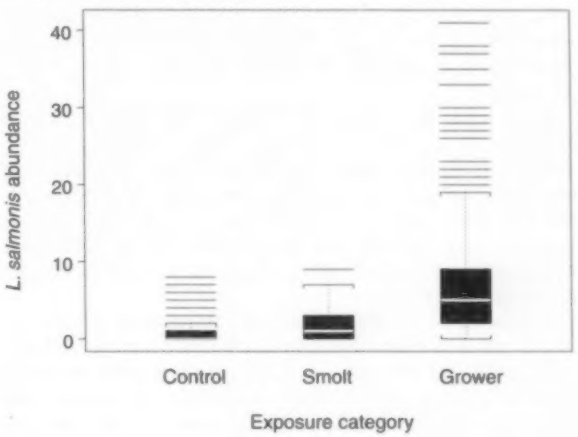


Fig. 5. Abundance of sea lice (*Lepeophtheirus salmonis*) on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the Broughton Archipelago for each of the three exposure categories: control, smolt, and grower. See Fig. 3 for interpretation of box plots.



sure status had no influence on *Caligus* abundance and then performed pairwise comparisons to search for specific differences.

Even with this potential conservatism, there remains strong evidence of differences in *Caligus* abundance among the different exposure categories (Broughton grower, Broughton smolt, Bella Bella grower, and the control sites) ($F = 13.85$, df = 3 and 19.4, $p < 0.0001$). Indeed, nowhere in the control areas did the mean *Caligus* count per fish exceed 0.04, and at all control sites outside the Broughton Archipelago, the mean *Caligus* count was uniformly less than 0.008. In addition, multiple comparisons of the means of each of the three impact categories (Table 2) and the combined mean for the control categories showed that the two categories with the highest observed mean count per fish, Bella Bella grower and Broughton smolt, were significantly higher than all the rest. By contrast, when we performed pairwise comparisons for means of control observations from the five geographic regions, there were no significant differences at the 5% level, even without any adjustment for multiple comparisons. Hence, chance variation cannot explain the higher *Caligus* incidence at the Bella Bella grower and Broughton grower sites.

Discussion

Our results do not support the hypothesis that the average abundance of sea lice on pink and chum salmon was unrelated to proximity to a salmon farm. In particular, the overall pattern of *L. salmonis* abundance we observed within the Broughton Archipelago counters the hypothesis that *L. salmonis* is naturally more abundant in the Broughton Archipelago than in the other regions sampled. Estimated abundances increased eightfold between control sites and those close to farms at the grower stage. While this study cannot provide a causal link among salmon farms, sea lice, and juvenile wild salmonid infection rates, five findings add

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Fig. 6. Comparison of abundance of sea lice (*Lepeophtheirus salmonis*) on pink (*Oncorhynchus gorbuscha*) vs. chum (*Oncorhynchus keta*) salmon. See Fig. 3 for interpretation of box plots.

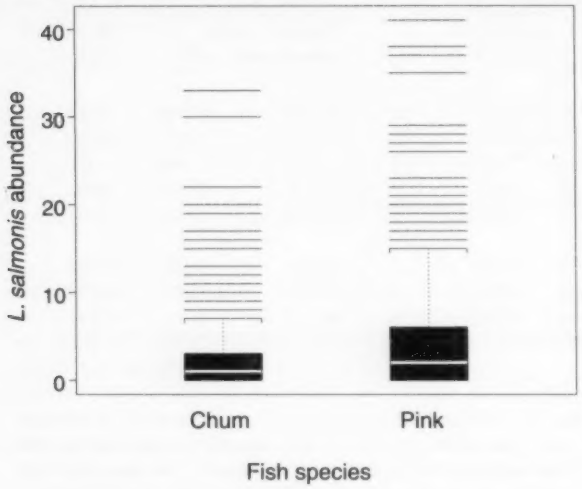

Table 3. The proportions of fish sampled in the Broughton Archipelago infected with more and less than 1.6 lice·(g host mass)$^{-1}$ for both pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon at the control sites (distant from salmon farms), a smolt salmon farm site, and the grower sites.

	Exposure category		
Infection rate	Control	Smolt exposed	Grower exposed
Pink			
Under 1.6 lice·g^{-1}	279	6	63
Over 1.6 lice·g^{-1}	90	5	375
Total	369	11	438
Proportion over	0.244	0.455	0.856
Chum			
Under 1.6 lice·g^{-1}	132	9	3
Over 1.6 lice·g^{-1}	36	17	50
Total	168	27	53
Proportion over	0.214	0.654	0.943

considerably to the concern that salmon farms are a major source of sea lice in the Broughton Archipelago and have significantly altered the population dynamics of sea lice in the region.

In all areas throughout the study period, there were substantially more lice near salmon farms, whereas in geographic areas where there were no farms, lice numbers were near zero. Second, the sustained dominance of juvenile sea lice life stages indicates that infective events were continuous and local. The fact that the juvenile (but not adult) lice abundances were significantly higher in the near-farm sites reinforces this point.

Third, we found that the highest occurrence of lice occurred not only near salmon farms, but also near those holding year 2 (grower) salmon. Although the formal statistical analysis showed that this may be a result of partial confounding with time effects, the number of sea lice per farm-salmon host has been reported to triple from year 1 to year 2 of a sea farm's production cycle in Scotland (Revie et al. 2002). Hence, if salmon farms were the source of lice on wild salmon, one would expect higher infection rates near grower sites than smolt sites.

Fourth, the anomalously high lice infection rates recorded in 2001 (Morton and Williams 2004) reoccurred in 2002. And finally, 90% of pink and chum salmon in the densely salmon-farmed waters of the Broughton Archipelago were infected at or above the level considered lethal (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997).

Both the 2001 and 2002 sea lice epizootics on wild juvenile salmon near salmon farms in B.C. share key characteristics with sea lice epizootics in Europe. The onset of this phenomenon in Pacific waters strongly suggests that a common variable between the two areas could be the arrival of novel, stationary, salmonid hosts into nearshore marine habitat. Salmon farms do offer sea lice ideal overwintering habitat not previously available. While salmon farms have been in operation in the Broughton Archipelago since 1987, the number of farms has increased since that time, and more recently, stocking densities have also increased to over one million Atlantic salmon per farm at some sites (Naylor et al. 2003). The number of lice larvae released by salmon farms has been calculated to increase with the number of salmon per farm (Heuch and Mo 2001).

While European sea lice studies benefit from access to sea lice counts on farm salmon, salmon farm companies do not release their sea lice infection rates by farm site in B.C. Therefore, we could not compare infection rates between adjacent wild and farmed salmon stocks; we could only look at how the number of sea lice varied near to and distant from salmon farms.

The differences in mean lice numbers between locations and over time were not merely artefacts of confounding with salinity and temperature differences. While *L. salmonis* survival is optimal at a salinity of 30‰ (Johnson and Albright 1991*b*) and copepodids avoid water with less than 20‰ (Heuch 1995), we found the highest numbers of lice in 28.6‰ and one of the lowest levels in water at 33.6‰. Although this study was not designed specifically to test the impact of salinity, its potential to confound the effects of proximity to fish farms can be evaluated. When salinity, temperature, and exposure categories were included in the statistical model, only the exposure category remained significant. Therefore, partial confounding with salinity and temperature cannot explain the increased abundance of lice caught near the fish farms. The overall low salinity values recorded in this study (less than 30‰) suggest that lice abundance could have been higher if salinity values had reached levels optimal for *L. salmonis* survival.

The sustained large number of juvenile-stage lice in this study provides evidence of continuous larval lice production somewhere within range of the fish we sampled. At 10.4 °C, sea lice would progress rapidly from newly hatched nauplii through the critical stage at which they must find a host (6–10 days). These observations are closely analogous to sea lice demographics near salmon farms elsewhere (Tully et al. 1993; Bjørn and Finstad 2002). Persistent lice production could not occur in the absence of a substantial salmonid host

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Table 4. Summary of model fits to *Lepeophtheirus salmonis* abundance data.

Dependent variable	Model	Effect	Degrees of freedom: Numerator	Denominator	*F*	*p*
Total	Full	Exposed	2	2.42	22.9	0.0267
		Week	9	44.8	6.61	<0.0001
		Week × exposed	10	47.9	2.59	0.0134
		Species	1	1112	0	0.8908
		Salinity	1	8.12	0.56	0.474
		Temperature	1	29.4	0.26	0.616
Total	Reduced	Exposed	2	5.84	26.58	0.0012
		Week	9	50.3	9.5	<0.0001
		Week × exposed	10	48.4	2.75	0.009
Adult	Reduced	Exposed	2	8.27	4.17	0.0559
		Week	9	40.4	4.4	0
		Week × exposed	10	40.6	1.3	0.2625
Juvenile	Reduced	Exposed	2	2.74	30.84	0.0132
		Week	9	52.6	8.61	<0.0001
		Week × exposed	10	50.6	2.72	0.009

Note: The full model is presented only for the totals. Because none of the three factors (species, salinity, or temperature) was ever significant in these models (smallest p value = 0.39), only reduced model results are presented for adults and juveniles.

Fig. 7. The presence of life stages of sea lice (*Lepeophtheirus salmonis*) found each week in the Broughton Archipelago: copepodid (solid), chalimus I–II (shaded), chalimus III–IV (hatched), adult (open).

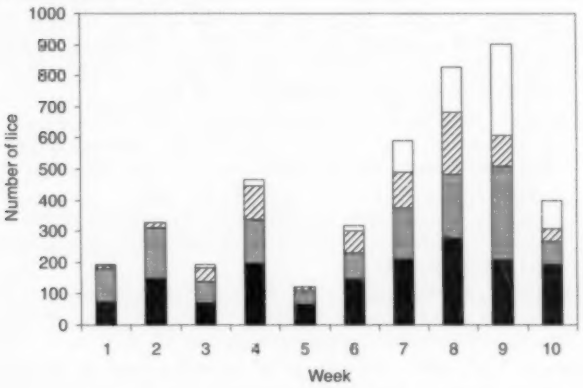
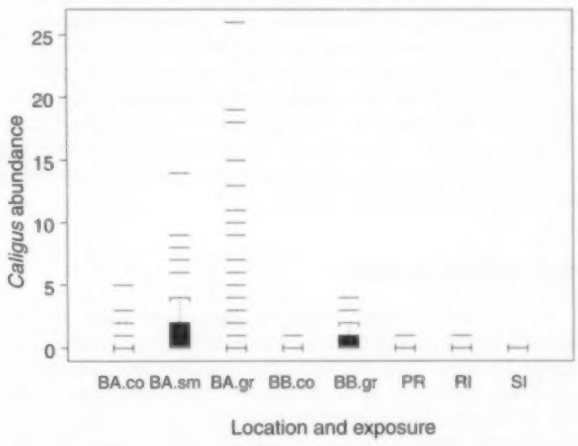


Fig. 8. Presentation of abundance of *Caligus* lice on juvenile salmon sampled in all five areas for all exposure categories. BA.co, Broughton Archipelago control (distant from salmon farm); BA.sm, Broughton Archipelago smolt site; BA.gr, Broughton Archipelago grower sites; BB.co, Bella Bella control (distant from salmon farm); BB.gr, Bella Bella grower sites; PR, Prince Rupert (no salmon farm in region); RI, Rivers Inlet (no salmon farm in region); SI, Smith Inlet (no salmon farm in region). See Fig. 3 for interpretation of box plots.



population within the Broughton Archipelago throughout the 10 weeks of this study. While there are some yearling chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon, steelhead (*Salmo gairdneri*), and cutthroat trout (*Salmo clarkia*), no reports of large wild salmonid populations could be found in this area (Glen Neidrauer, Department of Fisheries and Oceans patrolman, P.O. Simoom Sound, BC V0P 1S0, Canada, personal communication).

High numbers of a *Caligus* species in areas where farm salmon had been placed more recently (i.e., Bella Bella and the smolt site in the Broughton) correspond to what others have found (Hogans and Trudeau 1989). This non-salmon-specific, more generalist fish parasite may already be present in the new-farm environment as the farm stock arrive, and therefore may be capable of taking advantage of new hosts. *Lepeophtheirus salmonis* might only occur in pulses during the wild salmon spawning migrations in summer and fall.

There is evidence that sea trout, which inhabit the nearshore environment longer than Atlantic salmon (Johnstone et al. 1995), are more susceptible to sea lice in areas stocked with farm salmon than Atlantic salmon (R.S. McKinley, The University of British Columbia, 4160 Marine Drive, Vancouver, BC V7V 1N6, Canada, personal communication). Since pink salmon are also known to utilize the

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nearshore marine environment for a number of months (Bailey et al. 1975; Cooney et al. 1978), it is reasonable to expect this behaviour to similarly exacerbate susceptibility of pink salmon to sea lice.

Pink and chum salmon are much smaller than salmonids in the Atlantic studies at seawater entry, and this might be important in regards to degree of lethal impact from sea lice. For the first 3 weeks of this study, the fish sampled adjacent to salmon farms weighed substantially less than 1 g, but averaged 3.4 lice·fish^{-1}. The only lethal lice level known for salmonids is 0.75–1.6 mobile lice·(g host mass)$^{-1}$ (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997). Not all lice on these very young pink and chum salmon had reached their mobile stages, but by week 7 of the study, the mean mass was 0.9 g and the load was 1.8 mobile lice·(g host mass)$^{-1}$ (SD = 0.56). More research on sea lice pathogenicity to Pacific salmonids is paramount, but these numbers would seem solid ground for enacting a precautionary approach until the dynamic between sea lice and juvenile Pacific salmon is more fully understood.

In conclusion, heavy infestations of sea lice have been observed on juvenile pink salmon in the Broughton Archipelago in 2001 (Morton and Williams 2004) and pink and chum salmon in 2002. The evidence from both this study and European research points to a sea lice source in the vicinity of the fish farms. In the absence of any B.C. studies directed on sea lice in the salmon farms and therefore any means to relate lice on farm salmon to lice on wild salmon, there do not seem to be any direct tests possible for the concern that salmon farming is involved in this cycle of infections.

When the pink salmon stock examined in this study returned to spawn, their numbers were 87% lower than the parental stock (Gordon McEachen, Department of Fisheries and Oceans, Rm 150 – 1260 Shoppers' Row, Campbell River, BC V9W 2C8, Canada, personal communication). Declines in pink salmon returns in 2002 and 2003, known to have been heavily infected by sea lice as juveniles, point to serious concern for the continuance for some salmon populations in the Broughton Archipelago. Further research concerning sea lice dynamics in the Broughton Archipelago ecosystem and lethality of *L. salmonis* on juvenile salmonids is clearly an immediate priority.

Acknowledgements

We thank Dr. John Volpe for his contribution to this study's design, Neil Frazer for his contributions to the manuscript, Dr. Jens Christian Holst for his patience in addressing our many questions, Rolf Hicker for help with graphics, the David Suzuki Foundation for allowing us to analyze fish sampled by Dave Rolston in the Prince Rupert area, and the anonymous reviewers and others who improved this manuscript considerably. This work was partially funded by Tides Canada Foundation – Wild Salmon Fund and the Natural Sciences and Engineering Research Council of Canada.

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Effects of sex, stock, and environment on the shape of known-age Atlantic cod (*Gadus morhua*) otoliths

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Abstract: The effects of sex, stock, and environment on the shape of known-age Atlantic cod (*Gadus morhua*) otoliths from the Faroe Islands were investigated. Moreover, the feasibility of otolith shape analysis for stock identification was evaluated. The shape was described by using several normalized Fourier descriptors and morphometric variables. There were no consistent differences between the left and right otoliths and between sexes within different age classes, stocks, and environments. With our experimental design, we could evaluate the relative importance of genetic and environmental conditions (water temperature and diet regime) on otolith shape and morphometrics. Using otolith shape, cod individuals were significantly separated into Bank and Plateau stocks. Total classification success was between 79% and 85% between stocks and between 85% and 96% between environments for the different age classes. The significant differences in otolith shape between Faroe Bank and Faroe Plateau cod stocks provided a phenotypic basis for stock separation. Stock and environmental influences were substantial in determining the shape of cod otoliths.

Résumé : Nous avons examiné les effets du sexe, du stock et du milieu sur la forme de l'otolithe chez des morues franches (*Gadus morhua*) d'âge connu aux îles Féroé et évalué la valeur de l'analyse de la forme des otolithes pour l'identification des stocks. Plusieurs descripteurs de type Fourier normal et des variables morphométriques ont servi à décrire la forme. Il n'y a pas de différence constante entre les otolithes droits et gauches, ni entre les otolithes des deux sexes à l'intérieur d'une classe d'âge, d'un même stock ou d'un même environnement. Notre plan d'expérience nous permet de distinguer l'influence relative des facteurs génétiques et environnementaux (température de l'eau et régime alimentaire) sur la forme et la morphométrie des otolithes. D'après la forme des otolithes, il est possible de séparer de façon significative les individus des stocks Bank et Plateau. Le succès global de la classification est de 79 % à 85 % entre les stocks et de 85 % à 96 % entre les milieux pour les différentes classes d'âge. Les différences significatives de forme des otolithes des stocks Bank et Plateau de Féroé fournissent une base phénotypique pour la discrimination des stocks. Les influences du stock et de l'environnement sont d'importance dans la détermination de la forme des otolithes chez la morue.

[Traduit par la Rédaction]

Introduction

For most fish species, otoliths form a permanent record of life history events (Campana 1999). One of the visible internal features of otoliths is the alternation of optically distinct zones, usually interpreted to reflect the age of a fish (Williams and Bedford 1974). Otoliths grow throughout the entire life of an individual fish, are metabolically inert (Campana and Neilson 1985), and are routinely collected for stock assessment purposes (Beamish and Chilton 1982). The external characteristics of the otolith, such as shape and other morphometric features, reflect the developmental stage of the phenotype being mainly influenced by sex, age, year class, stock, and environment (Castonguay et al. 1991; Lombarte and Lleonart 1993; Begg and Brown 2000). Otolith shape is species specific and is less variable in growth than fish growth (L'Abee-Lund 1988). Therefore, the shape of the otolith appears to be an ideal marker for fish population affiliation and has been used to differentiate between stocks (Bird et al. 1986; Campana and Casselman 1993; Begg and Brown 2000). The presence of stock differences in otolith shape has been attributed to regional differences in fish metabolic activity that alter the growth of otoliths, determining the size and shape of individual oto-

Received 20 August 2002. Accepted 31 July 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 15 March 2004.
J17052

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 doi: 10.1139/F03-151 © 2004 NRC Canada

liths (Gauldie 1990; Gauldie and Nelson 1990; Smith 1992). However, as it is the case with all other meristic or morphometric identification procedures, the use of otolith shape analysis does not distinguish between genetic and environmentally induced differences (Campana and Casselmann 1993; Begg et al. 2000). Although there may also be a genetic contribution to otolith shape differences between stocks (Mosegaard et al. 1988), environmental factors are considered to be the major determinants of otolith growth (Begg at al. 2000). Nevertheless, otolith morphometrics have been shown to provide a phenotypic basis for stock separation that is a crucial step in fisheries management (Begg and Waldman 1999).

This paper investigates to what extent several factors affect the shape of Atlantic cod (*Gadus morhua*) otoliths as described by Fourier analysis and linear morphometrics. We evaluated the effect of body side, sex, age, stock, and environment on otolith linear and shape morphometrics. Age is considered to be one of the factors inducing large variation in otolith shape within stocks (Begg et al. 2000), and differences in otolith shape are due to the age effect rather than to stock differences (Castonguay et al. 1991). Moreover, because of the underlying importance of environmental factors for otolith growth, and therefore otolith shape (i.e., Begg et al. 2000), we also investigated the influence of different growing conditions (artificial against natural environment) on otolith shape and morphometrics.

The experimental design of this study attempts to evaluate the relative importance of genetic and environmental effects on growth and shape of otoliths. In particular, we focused on the utility of otolith shape for fish stock separation. Therefore, the feasibility of otolith shape analysis for stock identification of North Atlantic cod was evaluated together with the effect of stock and environment components on the shape of cod otoliths.

Materials and methods

Fish sampling

The Faroese Fisheries Laboratory and the Aquaculture Research Station initiated an enhancement programme for Atlantic cod in 1991 (Jákupsstovu and Reinert 1994; Fjallstein and Jákupsstovu 1999). Prespawning cod individuals (i.e., sexually mature cod preparing to spawn) were caught in 1994 using bottom trawls when the fish were assumed to be in or near their spawning grounds (fig. 16.1 in Fjallstein and Jákupsstovu 1999) on the Faroe Bank and the Faroe Plateau. These represent two discrete spawning stocks (Jákupsstovu and Reinert 1994) (Faroe Bank: latitude 61°10′, longitude 9°30′; Faroe Plateau: latitude 62°15′, longitude 8°10′). These cod individuals were later stripped for their eggs, and after incubation, both eggs and newly hatched cod larvae were transferred to tanks and mesh bags. Cod individuals from the two stocks were reared in tanks and in pen cages. When the juvenile cod reached about 1 year, they were tagged with Floy anchor tags (FD-68bc). Individuals to be released (Plateau) were tagged a couple of weeks before transportation to the respective locations. Individuals kept for rearing from the Bank and Plateau stocks were tagged and mixed in three cages comprising approximately half Bank stock and half Plateau stock in each cage. The pen cages were positioned at the sea surface, mounted with nets of similar mesh size with a depth of approximately 4 m and a diameter of 8 m. Each year, subsamples were taken from the pen cages between January and April.

A total of 49 992 age-1 individuals were released from the Faroe Bank in 1994. A total of 8408 age-1 individuals were released from the Faroe Plateau in 1995, while initially, 3500 from the Faroe Bank and 3000 from the Faroe Plateau were kept in pen cages until spring 2000. Individuals from the Faroe Bank pen cage (FBP) and from the Faroe Plateau pen cage (FPP) representing the two separate stocks were reared at the same growing conditions (temperature and food intake), while recaptured individuals from Faroe Plateau (FPR) represented the wild counterpart. For each fish, sex, total fish length, and wet weight were recorded to the nearest 1 mm and 1 g, respectively. Otoliths (both left and right sagittae) were removed from each individual sampled and stored in dry envelopes for shape analysis. Accuracy of age reading rarely exceeds 90% and is usually much lower (e.g., Kimura and Lyons 1991; Cardinale et al. 2000). Since previous studies have examined otolith shape using individuals of uncertain age (e.g., aged using traditional ageing techniques), known-age specimens were used in our study. This will provide a solid basis to distinguish among age classes and thus eliminate the bias due to age reading procedures. Recaptured fish were assigned to the nearest age class. Recaptures were during the entire year through commercial fisherman activity.

Otolith shape analysis

Otolith morphometrics and normalized Fourier descriptors (NFDs) of otolith outline shape were recorded using an image analysis system (IMAGIC) (Van Heel et al. 1996). Scanning of the otoliths was done using a standard protocol step for acquiring pictures using a software–hardware workstation consisting of a stereomicroscope equipped with digital camera connected to a computer. The otolith was cleaned using an ultrasound cleaner and placed under the stereomicroscope on a glass plate with the sulcus upwards. A 0.5× objective was used with a magnification of × 6.3 or × 8. The silhouette picture of each otolith was taken using the digital camera with transmitted light and saved as an image file.

Automatic two-dimensional contour finding

First, the histogram of the grey-scale digital silhouette input image (typically 562 × 768 pixels) was calculated and used to establish a proper binarization threshold following the method of Zack et al. (1977). The image was subjected to morphological filters to remove salt-and-pepper noise as well as annotations and other unwanted objects. Subsequent edge finding yielded the simple outline around the object. The contour was then traced to establish a successive chain sequence of contour points. Typically, around 2000 contour points were obtained.

NFDs

Otolith orientation was standardized by positioning each otolith with the sulcus side up and with the rostrum to the upper left (Fig. 1). Usually, a closed contour consists of a different number of points for different otoliths. For the subsequent two-dimensional fast Fourier transform, however, a

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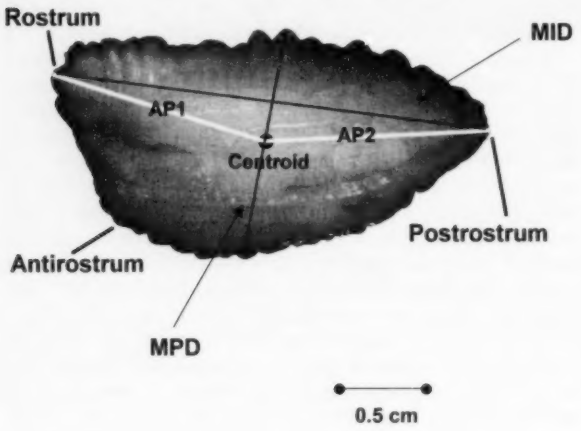
Fig. 1. Left otolith sagitta of a 4-year-old Atlantic cod from Faroe Bank. See Table 2 for definition of variables.



fixed number of points (2^N) is required, 4096 here. Therefore, the length of the contour line was determined and the position of 2^N equally spaced points along the contour was interpolated (Wallace and Wintz 1980). These new points were finally subjected to discrete two-dimensional fast Fourier transforms (Press et al. 1992) yielding the associated Fourier shape descriptors. The normalization of shape descriptors is achieved by standardizing the magnitude of the fundamental complex Fourier coefficient, also called fundamental amplitude. The fundamental amplitude can be envisioned as the radius of a circle that best fits the contour. Consequently, the original magnitude of the fundamental amplitude contains all of the original otolith size information as a single parameter. Thus, both shape and size descriptors are separately available. To account for different magnification settings of the microscope, the fundamental amplitude is finally multiplied with the magnification correction (M_{corr}) to give the size factor (SF):

$$SF \sim M_{corr} \|A(1)\| = M_{corr} \sqrt{A_{Re}(1)^2 + A_{Im}(1)^2}$$

where $\|A(1)\|$ is the magnitude of the fundamental complex Fourier coefficient (fundamental amplitude) and $A_{Re}(1)$ and $A_{Im}(1)$ are the real and imaginary parts of the fundamental complex Fourier coefficient. All procedures have been implemented as commands in the context of the IMAGIC suite of programs (Van Heel et al. 1996, 2000). The NFDs were normalized for orientation with a two-phase IMAGIC standard procedure and for size by using the amplitude of the fundamental harmonic. The first 68 harmonics were then used to describe each fast Fourier transform.

Geometrical and nongeometrical otolith descriptors and their definition

The following variables were recorded for each otolith pair using the IMAGIC image analysis procedures: area (OA), contour length (OC), length measured as the length of the maximum internal distance (MID), width measured as the length of the longest axis perpendicular to the maximum internal distance (MPD), the distance between the centroid (the centroid is determined as the centre of mass of the polygon defined by the contour points) of the otolith and the rostrum (AP1), the distance between the centroid of the otolith and the postrostrum (AP2), and the angle between AP1 and AP2 (AB). It is worth mentioning that MID is not the same as the usual measure of otolith length (i.e., the length along the long axis). Each otolith was also weighed to the nearest 0.1 mg. Finally, we estimated the ratio of otolith weight to fish length. All linear variables were in measured in millimetres.

Correlations between different geometric and nongeometric otolith descriptors were calculated. To analyse individual variability of these descriptors, we analysed the correlation between features in a subset of the cod otolith collection with right and mirrored left otolith images from the same fish ($n = 664$); the correlations were expressed as r^2 values. We also calculated the right–left correlations after scaling by MID^{-1} for all of the linear measures OC, MPD, AP1, and AP2 as well as the invariant AB, and further, OA was square root transformed.

Data analysis

The condition of cod individuals was estimated using K', defined as

$$K' = FW/FL^b \times 100$$

where FW is fish weight, FL is fish length, and b is a constant determined from the length–weight relationship

$$FW = aFL^b$$

This factor seems to perform adequately when data on body height are not available. Moreover, it is better than the traditional K where b is assumed to be equal to 3 (Richter et al. 2000). Differences in condition were tested using ANOVA.

All the measured otolith morphometric variables were tested for assumptions of normality and homogeneous variance using the Shapiro–Wilks W test (Shapiro et al. 1968) and the Hartley F_{max} statistic (Sokal and Rohlf 1995), respectively. Tests were computed for each selected variable among age classes, stocks, and environments. If the W statistic is significant, then the hypothesis that the respective distribution is normal should be rejected. ANCOVA and the homogeneity of slope test (Sokal and Rohlf 1995) were then used to estimate the effect of otolith length on the magnitude of each variable. If the interaction between the stock or environment and otolith length is significant for a given variable, then the variable has to be excluded because the sample cannot be corrected (in a consistent manner) for a variable-sized otolith (Begg and Brown 2000). This is fundamental because otherwise, the detected differences could exclusively be related to the size of the otolith and not to any other stock or environmental effect. The remaining variables were tested for correlation with otolith length. If a significant correlation exists between a variable and otolith length, significant intersample differences can arise from differences in length frequency among samples. Thus, all variables recognized as being significantly correlated with otolith length were corrected for otolith length by using the respective common within-group slope (b). This was done using the following formula:

$$\text{Corrected } V_i = \text{Old } V_i - b\text{MID}$$

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where V_i is the variable analysed. The effect of otolith length was removed from the variables instead of fish length because, as suggested by Campana and Casselman (1993), otolith length is unaffected by intersample differences in preservation, shrinkage, and distortion. Moreover, otolith length and fish length are usually strongly correlated (r^2 = 0.85 in this study). The correction was not applied to AB and all NFDs, since they represented size-independent variables.

MANOVA was used to analyse otolith shape differences between body side and sexes for samples from the same stock, environment, and age class by using the otolith length corrected otolith morphometric variables and the NFDs. One-way ANOVA (unbalanced design, fixed effect) was used to inspect each variable and define any significant difference estimated by MANOVA. Tukey's honestly significant difference test for unequal sample size was used for a posteriori comparisons of each significant variable.

Forward stepwise canonical discriminant analysis was used to separate cod from different stocks (Faroe Bank and Faroe Plateau) and different environments (pen cage and wild cod individuals from Faroe Plateau). The analysis was conducted for each age class separately because the shape of the cod otoliths is strongly influenced by the age of the fish (Campana and Casselman 1993). In this way, any confounding variation attributable to differences in the ages of the samples was removed (Begg and Brown 2000). The significant canonical variate (CanVar) derived by each analysis represented the optimal combination of morphometric variables and NFDs that provides the best overall discrimination between samples (Begg et al. 2000). One-way ANOVA (unbalanced design, fixed effect) was used to analyse differences in the CanVar scores, and jackknifed cross-validation procedures were used to calculate an unbiased estimation of classification success (SPSS Inc. 1999). The significance level was set at 0.05 for all the statistical tests used. Bonferroni adjustment for multiple tests was not used for simultaneous comparisons, since it has recently stated been that it is, at best, unnecessary and, at worst, deleterious to sound statistical inference (Perneger 1998). The likelihood of type II errors is increased, so that truly important differences are deemed nonsignificant. Simply describing what tests of significance have been performed, and why, is generally considered the best way of dealing with multiple comparisons (Perneger 1998). SPSS (SPSS Inc. 1999), S-PLUS (MathSoft Inc. 1999), and Statistica computer software (Statsoft, Inc. 1995) were used for the statistical analysis.

Results

The numbers of fish released and recaptured during the experiment are given in Table 1. The number of individuals recaptured was very low for Faroe Bank; thus, they were excluded from statistical analysis. Length frequency distributions of FBP and FPP matched by age group were not statistically different (Kolmogorov–Smirnov test, $p > 0.05$). On the other hand, length frequency distributions of FPP and FPR were significantly different (Kolmogorov–Smirnov test, $p < 0.05$). Cod individuals reared in the same controlled environment but belonging to different stocks (FBP and FPP) showed no statistical differences in mean condition factor (ANOVA, $p > 0.05$). However, the condition of fish differed statistically among individuals of the same stock that were growing in different environmental conditions (FPP and FPR) (ANOVA, $p < 0.05$).

Table 1. Total number of Atlantic cod released and recaptured for each stock during the experiment.

	Faroe Plateau		Faroe Bank	
Year	Released	Recaptured	Released	Recaptured
1994			49 992	13
1995	8408	183		11
1996		571		23
1997		210		86
1998		64		98
1999		7		22
2000		4		7
2001		1		1
2002		0		0

There were no consistent differences between the left and right otolith and between sexes (MANOVA, $p >> 0.05$) for all of the variables investigated within different age classes, stocks, and environments. Therefore, we used the left otolith when it was available and the right from those individuals where the left was not present or utilizable. The amount of discarded, damaged, or crystalline otoliths was less than 5% of all samples. Sexes were merged to increase the sample size used in the statistical analysis. Each variable in at least one age class was not normally distributed (Shapiro–Wilks W test; $p < 0.05$) and none of the variables, except the ratio of otolith weight to fish length, had equal variance within all age classes (Hartley F_{max} statistic, $p < 0.05$). Because parametric assumptions were not satisfied, these variables were $\log_e$ transformed prior to statistical analysis. Following logarithmic transformation, all variables conformed to parametric statistical assumptions. Concerning differences between stocks, a significant interaction between stock and otolith length for AP2 was found (ANCOVA, homogeneity of slope test, $p = 0.02$) (Table 2). Thus, AP2 was excluded from the stock differentiation analysis. All of the remaining variables were significantly correlated with MID and were therefore corrected for otolith length using their respective within-group slope (Table 2). For differences between environments, we found a significant interaction between environment and otolith length for all of the variables examined (ANCOVA, homogeneity of slope test, $p < 0.05$) except MPD and AB (Table 3). Therefore, those variables were excluded from the environment differentiation analysis. The two remaining variables (MPD and AB) were significantly correlated with MID. MPDs were therefore corrected for otolith length using their respective within-group slope (Table 3). As mentioned before, AB was not corrected because it is a size-invariant shape feature.

ANOVA showed significant differences between the different stocks, among the same age classes, in several of NFDs and two of the morphometric variables (MPD and AB). Some of the NFDs were consistently different between stocks in all age classes. ANOVA also showed significant differences in otolith shape between individuals of the same age and stock that were living under different growing con-

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Table 2. Otolith morphometric variables significantly correlated with otolith length (MID) and the corresponding regression coefficients (*b*) required standardizing the variables for otolith length in the Atlantic cod stock separation analysis.

	MID × stock			MID			
Otolith morphometric variable	*F*	*n*	*p*	*F*	*n*	*p*	*b*
OW	0.42	440	0.52	4 251.18	440	**<0.01**	3.51
OC	2.15	440	0.14	6 587.16	440	**<0.01**	0.98
OA	0.02	440	0.88	9 528.93	440	**<0.01**	2.22
MPD	0.09	440	0.76	2 854.66	440	**<0.01**	1.25
AP1	3.17	440	0.08	27 089.36	440	**<0.01**	1.01
AP2	5.07	440	**0.02**				
AB	2.83	440	0.09	176.77	440	**<0.01**	0.09
Size factor	0.40	440	0.53	4 241.18	440	**<0.01**	1.08
OW/FL	1.35	440	0.25	1 588.45	440	**<0.01**	1.07

Note: Significant values are in bold. OW, otolith weight; OC, otolith contour length; OA, otolith area; MID, length measured as the length of the maximum internal distance; MPD, width measured as the length of the longest axis perpendicular to MID; AP1, distance between the centroid (the centroid is determined as the centre of mass of the polygon defined by the contour points) of the otolith and the rostrum; AP2, distance between the centroid of the otolith and the postrostrum; AB, angle between AP1 and AP2; OW/FL, ratio of otolith weight to fish length. See text for details on units of measurement.

Table 3. Otolith morphometrics variables significantly correlated with otolith length (MID) and the corresponding regression coefficients (*b*) required standardizing the variables for otolith length in the Atlantic cod environment separation analysis.

	MID × environment			MID			
Otolithic morphometric variable	*F*	*n*	*p*	*F*	*n*	*p*	*b*
OW	5.24	501	**0.02**				
OC	14.66	501	**<0.01**				
OA	6.37	501	**<0.01**				
MPD	3.37	501	0.07	2356.86		**<0.01**	1.16
AP1	31.85	501	**<0.01**				
AP2	21.01	501	**<0.01**				
AB	2.36	501	**0.13**	95.67		**<0.01**	0.06
Size factor	6.08	501	**0.01**				
OW/FL	7.58	501	**0.01**				

Note: Significant values are in bold. See Table 2 for definition of variables, and see text for details on units of measurement.

ditions. Some of the NFDs but also all morphometric variables (MPD, AB, and otolith weight) were consistently different between stocks in all age classes. Again, several NFDs and two morphometric variables (MPD and AB) were significantly different between environments. The two most significantly different NFDs and morphometric variables between stocks (FBP and FPP) and environment (FPP and FPR) for each age class of cod are given in Fig. 2.

Discriminant analysis revealed that, combining otolith shape and otolith morphometric variables, cod individuals were correctly assigned to the two stocks Faroe Bank and Faroe Plateau (Fig. 3). CanVars were significantly different (ANOVA) between stocks, although a shift in the sign of CanVar was observed between age class 3 and age classes 2, 4, and 5. For each age class, several but different NFDs and MPD (age class 2), otolith weight (age class 4), and otolith weight and OC (age class 5) were used in discriminating between stocks. Total classification success after jackknifed cross-validation was between 78.8% and 84.7% for the different age classes (Table 4).

Several NFDs and MPD were used for classification of cod individuals of the same stock growing in different environmental conditions (Fig. 4). CanVars were significantly different (ANOVA) between different environmental conditions, although, as for stock separation analysis, a shift in the sign of CanVar was observed between age class 2 and age classes 3 and 4. MPD was selected only in age class 3 as a discriminant factor, while none of the NFDs was consistent between the age classes considered. Total classification success after jackknifed cross-validation was between 84.9% and 96.3% for the different age classes (Table 4).

The definition of individual landmarks underlying the morphometric features is highly influenced by subtle shape differences such as the exact position of an individual lobe. To investigate the within-individual variation of these features, some of them highly significant in the assignment analyses above, a comparison between right and mirrored left images was performed by correlation analysis. Contrary to the NFDs, the linear morphometric features were corrected for size except for the angle AB, which was considered to be

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Fig. 2. Error bar plot (mean ± SE) of (*a* and *c*) two normal Fourier descriptors (NFD) and (*b* and *d*) morphometrics variables (mm) that were most significantly different between stocks (Faroe Bank pen cage (FBP) and Faroe Plateau pen cage (FPP)) and environment (FPP and Faroe Plateau recapture (FPR)) per each age class of Atlantic cod. Solid circles, FPP; open circles, FBP; shaded circles, FPR. See Table 2 for definitions of variables.

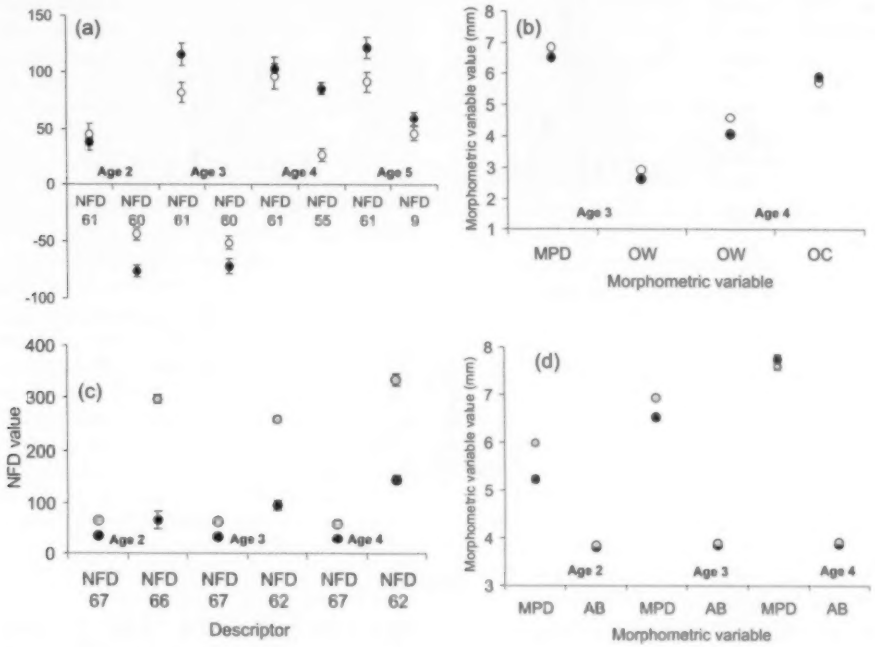
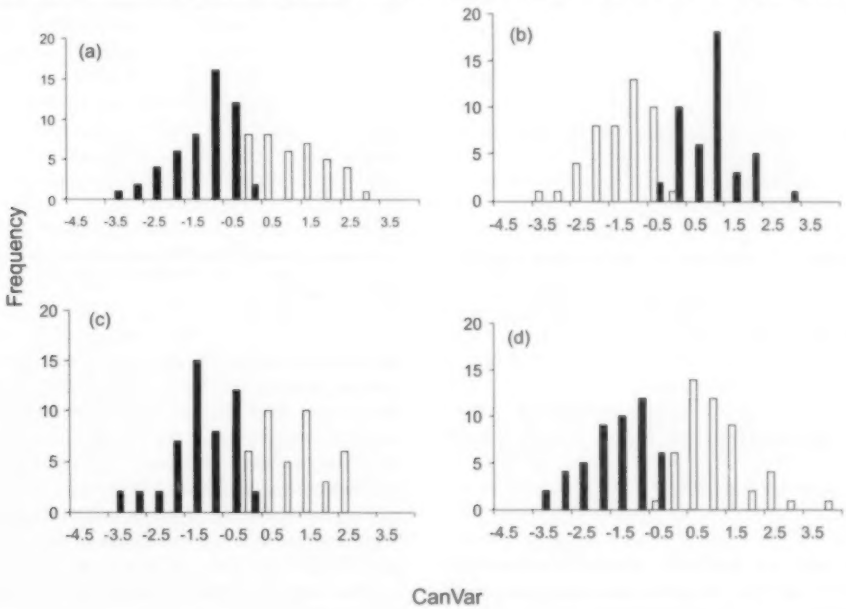


Fig. 3. Age-specific discrimination between Faroe Bank pen cage (FBP) and Faroe Plateau pen cage (FPP) (stock separation) Atlantic cod samples based on first canonical variate (CanVar) scores for ages (*a*) 2, (*b*) 3, (*c*) 4, and (*d*) 5. Solid bars, FPP; open bars, FBP.



size invariant in the present case. Both uncorrected and corrected values were compared. All morphometric features exhibited high correlation with MID (r^2 = 0.83, 0.98, 0.98, 0.93, and 0.95 for MPD, AP1, AP2, OC, and $OA^{0.5}$, respectively) except AB, which had an r^2 of 0.19. Individual right–left correlations of the morphometric features MID, $OA^{0.5}$, OC, MPD, AP1, and AP2 were high except for the invariant angle AB. On the other hand, the right–left correlations after

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Fig. 4. Age-specific discrimination between Faroe Plateau pen cage (FPP) and Faroe Plateau recapture (FPR) (environment separation) Atlantic cod samples based on first canonical variate (CanVar) scores for ages (*a*) 2, (*b*) 3, and (*c*) 4. Solid bars, FPR; open bars, FPP.

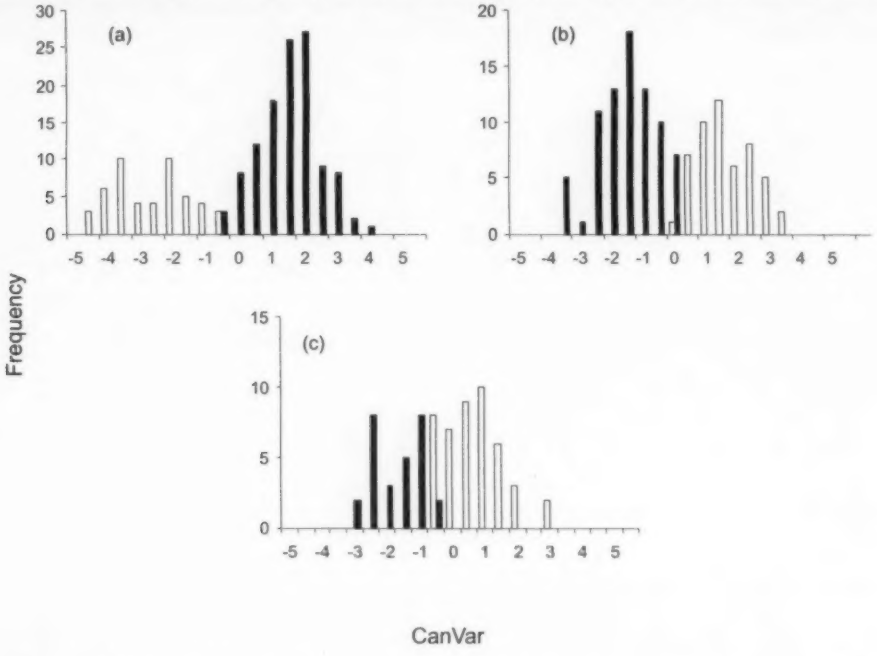

Table 4. Age-specific jackknifed cross-validation classification success for Atlantic cod stock and environment separation analysis.

	Age 2	Age 3	Age 4	Age 5
Correct classification of cod stocks by age class, %				
n	90	91	90	98
FBP	75.0	77.3	76.9	84.0
FPP	87.0	74.5	84.3	85.4
Total	81.1	75.8	81.1	84.7
Correct classification of cod environments by age class, %				
n	163	129	73	
FPP	95.7	93.6	82.4	
FPR	96.6	87.8	90.9	
Total	96.3	89.9	84.9	

Note: Faroe Bank pen cage (FBP) and Faroe Plateau pen cage (FPP) are the two separate stocks reared in the same growing conditions (temperature and food intake), whereas recaptured individuals from Faroe Plateau (FPR) represented the wild counterpart.

Table 5. Correlation within Atlantic cod otolith morphometric variables between left and mirrored right otolith images and between left and mirrored right otolith images adjusted for MID^{-1} for all listed variables.

Variable	r^2 with MID	r^2 between right and left otolith	r^2 adjusted for MID^{-1}
MID	—	0.97	—
MPD	0.83	0.97	0.75
AP1	0.98	0.97	0.49
AP2	0.98	0.96	0.48
OC	0.93	0.95	0.47
$OA^{0.5}$	0.95	0.99	0.74
AB	0.19	0.40	0.94

Note: See Table 2 for definition of variables, and see text for details on units of measurement.

scaling $OA^{0.5}$, OC, MPD, AP1, AP2, and AB by MID^{-1} showed drastically decreased values except for AB, which increased (Table 5).

Discussion

The concept of stock is a useful taxonomic grouping that is considered crucial for the purposes of management of fisheries resources (Begg and Waldman 1999). Larkin (1972) considered a stock to be a production or management unit where the stock concept describes the characteristics of the units assumed homogeneous for management objectives (Begg and Waldman 1999). Ricker (1981) highlighted that the understanding of the stock structure of a given fish species is important for outlining pertinent management regulations in those fisheries where multiple stocks are differentially exploited at the same time. Therefore, several studies have been conducted with the purpose of distinguishing between individuals belonging to different stock units, and recently, the need for a holistic approach (involving a broad spectrum of complementary techniques) has been suggested (for a review, see Begg and Waldman 1999). In particular, several authors have investigated the shape of otoliths to assess its use for distinguishing among different stocks (i.e., Smith 1992; Friedland and Reddin 1994; Bolles and Begg 2000).

The use of the otolith has been advocated because otoliths are routinely collected and used for ageing in traditional

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stock assessment (see Cardinale et al. 2000), and thus, their complementary use in stock identification is both logical and efficient (Friedland and Reddin 1994). However, several confounding effects have been pointed out: sex, year class, and age among others (Simoneau et al. 2000). Nevertheless, previous studies have usually used individuals of unknown age, adding ageing uncertainty as an additional confounding effect. In our study, this bias has been completely eliminated through the use of known-age fish. At the same time, otoliths of different sexes did not show any differences in otolith shape, as shown in other studies (i.e., Castonguay et al. 1991; Begg et al. 2000; Simoneau et al. 2000), excluding this variable as a confounding effect. Moreover, we used a single year class followed in time and we kept age classes separated to rule out those variables also acting as confounding factors in otolith shape analysis.

Another important confounding effect is represented by the impact of allometric growth on otolith shape, and this has never been quantified (Simoneau et al. 2000). However, various standardization techniques have been applied to correct for length effect, although these techniques do not completely correct for otolith size effect (Simoneau et al. 2000). In our study, Fourier descriptors were normalized for otolith length (i.e., estimated for an ideal otolith of the same size), and otolith morphometrics were also corrected for otolith length to highly reduce, if not eliminate, this confounding factor in the analysis. As previously mentioned, the angle AB between apex vectors is a size-invariant shape measure. It compares therefore best with the normalized Fourier shape descriptors that were introduced as such into the analysis. However, one could have decided to apply corrections to AB for otolith length primarily to stay consistent with literature procedures (i.e., Simoneau et al. 2000). However, since the within-group slope for AB is small ($b = 0.06$), the expected effect is small. We have checked in a separate analysis that the use of corrected or uncorrected AB has no significant effect on the results. Moreover, since fish length distributions were not statistically different for the two stocks, length effect was already strongly reduced in our study. Thus, several sources of uncertainty were eliminated or minimized in this study, providing a solid basis for discussing highlighted real differences in otolith shape between stocks and environments as not being due to sample differences.

Several studies have indicated that otolith shape differences between stocks are likely to be caused by both environmental and stock (i.e., genetic) influences, although it is unclear to what extent phenotype (environmental conditions affecting plausibly growth rates) and genotype affect otolith shape (Begg et al. 2000; Simoneau et al. 2000). Nevertheless, different studies suggested that environmental factors are major determinants of otolith growth, and therefore, differences in otolith shape are essentially mediated by differences in water temperature and feeding conditions (Campana and Casselman 1993; Begg et al. 2000). The experimental design in our study provided an interesting tool, helpful for evaluating the relative importance of genetic and environmental conditions (water temperature and diet) on otolith shape and morphometrics. Individuals belonging to different stocks but growing at the same temperature and under the same feeding conditions (i.e., condition factor did not differ statistically between those two groups) revealed otolith morphometrics with similar growth rates but a significantly different otolith shape as described by the NFDs. On the other hand, individuals belonging to the same stock but growing in different temperature and feeding regimes (i.e., different growing conditions) had otoliths where all morphometrics characters (except MPD and AB) significantly differed with respect to growth rates (slopes). As a consequence, the shape of the otoliths (described by the NFDs) was also significantly affected. Differences in growing conditions were also evident analysing the condition factor of those individuals reared in cages under better feeding conditions compared with wild cod individuals (i.e., condition factor did differ statistically between these two groups being higher for individuals reared in cages).

Because of the high significance of some of the morphometric characters used in this study, such as MID, MPD, AP1, AP2, and AB, we want to point out some limitations of these descriptors. Except for AB, the descriptors are distances between specific contour points or the centroid (geometrical landmarks). Whereas the centroid is defined by all contour points and is therefore relatively stable with respect to small contour variations, the extreme points on the contour are critical, meaning that slight contour variations may have a large impact on the actual position of an extreme point. For example, the presence and specific shape of a single lobe can influence the position of an extreme point, which in turn determines MID but also the angle between apex vectors (AB). Since some of the features depend on critical assignment of specific landmark points, the actual values are prone to measurement uncertainty. An estimate for the magnitude of the combined effects was obtained from the correlation between features in the left and mirrored right otolith images. To highlight the differences between the different features, correlation values are shown for untransformed and corrected variables, i.e., scaled to otolith length MID according to their appropriate dimension. It is quite clear that the left–right correlation r^2 of AP1 as well as of AP2 decreases by scaling to otolith length from very high to low. On the other hand, AB, which is born size invariant, increases from low to very high by the same scaling. Without scaling, AP1 and AP2, although prone to some uncertainty in landmark estimation, show the same magnitude in correlation between left and right otolith measurements as OA and MPD. The low correlation in AP1, AP2, and OC after scaling is probably due to their high correlation with MID rather than a high true left–right variation as in the estimated angle AB, which also has a very low correlation with MID. The effects of local contour variation on landmark assignment are unwanted but difficult to eliminate. One approach would be to use an automatic estimation from a smoothed contour rather than, as we did, using geometrical identification of points on the high-detail original contour line. Since smoothing of a contour is easily performed in Fourier space and already available with the software used, further studies in that direction are planned.

Because of common garden rearing conditions, essentially only inherent stock differences should exist at the time of release. After separation between reared and released individuals, increasing environmentally induced shape differences should develop within and between stocks. In the present case, because of very low recapture rates from the Faroe

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Bank stock, only an incomplete statistical comparison was available and those fish were not included in the statistical analysis. Moreover, because of within-age-group standardization, comparing CanVar scores between different age groups may be considered as nonsense. Nevertheless, we observed a general shift in the sign of the CanVar scores from younger to older fish in both stock and environment separation analysis. The scrutiny of the individual variables that were responsible for stock and environment separation did not provide any clues for interpreting the observed shift. However, it should be noted that differences in the release date among individuals of the same age influenced the length and weight at release as well as mortality rates and therefore the amount of rearing environment influence accumulated in the otolith shape. Moreover, large and (or) fast-growing individuals, being more vulnerable to early recapture by commercial fishing, may have influenced the otolith shape results differently in the younger than in the older age groups.

These results indicated that while genetic differences influence the shape of the otolith itself (under the same experimental conditions), the environmental effects essentially alter the rates of otolith growth, which in turn modifies otolith shape. This demonstrates that both genetic and environmental influences are substantial in determining the shape of the otolith and that different genotypes induce important differences in otolith shape. This strengthens the validity of shape analysis for stock identification where both phenotypic- and genetic-induced characters are used simultaneously. On the other hand, as stressed by Casselman et al. (1981), phenotypic-based characters are just as reliable for stock identification as genetic-based characters.

This study confirms the hypothesis that otolith shape analysis may assist in the development of a consistent identification of exploited fish stocks. This concept is valid, although because of confounding growth effects (i.e., year-class effect resulting from variable growth conditions), discriminant functions need to be recalculated each year for each of the major age classes in the population (Begg and Brown 2000). Moreover, it helps to elucidate the different impact of genetic and phenotypic effects on otolith morphology, demonstrating where these factors act to determine the observed differences. This information is fundamental if otolith shape is to be used in the future as an effective tool for management of fisheries resources.

Acknowledgments

We are grateful to the Faroese Fisheries Laboratory for supplying the cod otoliths and valuable background information. We also thank Gavin Begg for statistical advice. This study was partially financed by the European Commission, Directorate General Fisheries, within the project Fish Ageing by Otolith Shape Analysis (FAIR CT97-3402).

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Using underwater video to directly estimate gear selectivity: the retention probability for walleye (*Sander vitreus*) in gill nets

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Abstract: We developed a new approach for directly quantifying selection parameters for fishing gear using a dual underwater video camera apparatus and employed the method to estimate gill net retention probability for walleye (*Sander vitreus*). The method allows observation of fish behavior around fishing gear and estimation of the absolute probability of fish encountering, contacting, or being retained by the gear. We demonstrated the applicability of this method by quantifying the probability that walleye were retained in multifilament nylon gill nets after contacting the nets. Walleye with total lengths 2.49 times the perimeter of the mesh were most likely to be retained, and retention probability peaked at 0.60 (95% confidence interval 0.41–0.90), meaning 40% of walleye that were the ideal size for a given mesh escaped after contacting the net. Our empirically derived retention curve exhibited a steep ascending limb and strong positive skew because of walleye morphology and the tendency for larger walleye to be captured by tangling. Most walleye that avoided capture did not fully enter the mesh or backed out of the mesh after they became temporarily wedged or tangled.

Résumé : Nous avons mis au point une méthode nouvelle pour quantifier les paramètres de sélection d'engins de pêche qui utilise une paire de caméras vidéo sous-marines et nous l'avons appliquée à l'estimation de la rétention de dorés jaunes (*Sander vitreus*) dans un filet maillant. La méthode permet d'observer le comportement des poissons aux alentours du filet et d'estimer la probabilité absolue que les poissons rencontrent et touchent l'engin de pêche et soient retenus par lui. Nous démontrons l'efficacité de la méthode en calculant la probabilité que les dorés jaunes soient retenus par des filets maillants en multifilament de nylon une fois qu'ils sont entrés en contact avec eux. Les dorés dont la longueur totale représente 2,49 fois le périmètre de la maille sont les plus susceptibles d'être capturés et la probabilité de rétention atteint un sommet de 0,60 (intervalle de confiance de 95 %, 0,41–0,90), ce qui indique que 40 % des dorés de taille idéale pour une grandeur de maille donnée réussissent à s'échapper après avoir touché au filet. La courbe de rétention obtenue empiriquement possède une partie ascendante à forte pente et une asymétrie positive importante à cause de la morphologie des dorés et parce que les grands dorés ont tendance à se prendre par enchevêtrement. La plupart des dorés qui réussissent à éviter la capture n'entrent pas complètement dans le trou de la maille ou alors reculent après avoir été temporairement coincés ou enchevêtrés.

[Traduit par la Rédaction]

Introduction

Fishing gears typically catch some sizes and species of fish more efficiently than others. Selection is defined as any process that causes the probability of capture to vary with the characteristics of the fish (Lucas et al. 1960; Hamley 1975). A quantitative expression of selection is termed selectivity, which traditionally means selection by size (Lucas et al. 1960). Selection can occur at different stages of the capture process, and collectively these selective processes determine catchability, or the proportion of a stock removed with a given amount of fishing effort (Ricker 1975). If the catchability of the gear is known, population abundance can be estimated from catch data. Catchability of fishing gear, such as gill nets, has been estimated using both direct and indirect approaches. Direct estimates can be made when the number and sizes of fish in a population (or the number subjected to fishing) and the number of each size captured with a given amount of effort are known. Direct estimates of catchability have been produced using mark-and-recapture techniques to estimate population size (Hamley and Regier 1973) or by stocking known numbers of fish (Jensen 1995) and then subjecting the population to fishing. Indirect estimates of catchability can be made using a variety of statistical techniques that do not require the number of fish to be known, but rely on various assumptions about the relative shape and amplitude of selectivity curves.

Investigators have broken catchability of gill nets into various components to represent the sequence of events leading to capture and to define the selective processes occurring at each stage. A problem with breaking catchability into multiple components is that these components become con-

Received 7 October 2002. Accepted 30 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 15 March 2003.
J17130

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 doi: 10.1139/F03-166 © 2004 NRC Canada

founded and only relative probabilities for each component can be estimated. Rudstam et al. (1984) and Spangler and Collins (1992) assumed larger fish were more likely to encounter the gear because they have higher swimming speeds and thus cover more area per unit of time. These authors separated catchability into two selective processes: (1) the probability a fish would encounter the net, where they defined encounter as a fish contacting the net and (2) the probability the fish would be retained after encountering the net. Anderson (1998) separated catchability into three selective processes: (1) encounter — the probability a fish will approach the net close enough to detect it; (2) contact — the probability a fish that encounters the net will swim into it; and (3) retention — the probability a fish that contacts the net will be captured. We use Anderson's (1998) definitions of encounter, contact, and retention throughout this paper.

Underwater surveillance of deployed fishing gear can be used to directly quantify selective processes. Using underwater video cameras and recently developed video analysis techniques (Hughes and Kelly 1996), it is possible to count the number of fish that encounter, contact, and are ultimately captured in a gear or some portion of it and estimate their sizes. Underwater video has been used to observe reactions of Atlantic salmon (*Salmo salar*) and whitefish (*Coregonus lavaretus*) to modified trap nets (Toivonen and Hudd 1993). Matsuoka et al. (1997) used underwater video to observe the behavior of prawns and finfish in an ocean seine while quantifying selectivity with pocket and cover nets. To our knowledge, no studies have used video cameras to directly quantify size selectivity of fishing gear.

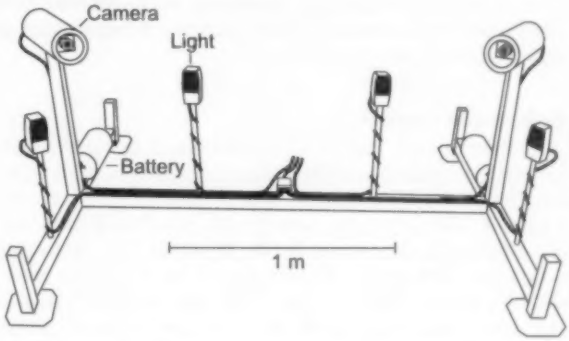
The purpose of this paper is to describe a new approach to directly quantify the selective processes for fishing gear and demonstrate its applicability by estimating the retention component for walleye (*Sander vitreus*) gill net selectivity models. Our primary goal is to develop a method to count absolute numbers and measure sizes of fish encountering a gear and (or) the probability that those fish will contact or be captured by the gear. Our second goal is to test the methodology by determining the probability that walleye are retained after contacting multifilament nylon gill nets and describe the methods of capture and behaviors that lead to escape from the nets. Finally, we demonstrate a potential use for this approach in testing indirectly estimated selectivity models by comparing the fit of our empirically derived retention curve to the retention function from Anderson's (1998) walleye gill net selectivity model.

Methods

General methodology

The general methodology requires two or more underwater video cameras to monitor deployed fishing gear and capture images of fish that approach, contact, and become captured by the gear. We developed a camera platform that was adjustable, yet could be transported and deployed next to fishing gear while maintaining the relative position of the two cameras. Our apparatus consisted of two high-resolution monochrome video cameras (M-370; Sony Corp., New York) in waterproof enclosures mounted on an aluminum frame along with four waterproof halogen lights (Ultra-Lights; ROS Inc., San Diego, Calif.) (Fig. 1). The lights were filtered with infrared glass (RG780; Schott Glass, Elmsford, N.Y.), allowing only infrared wavelengths (>780 nm) to pass. These wavelengths are outside the range detectable by the visual pigments of fish, but are detectable by monochrome video cameras. The video cameras were powered by 12-V batteries placed in waterproof housings that were mounted on the aluminum frame. The frame was adjusted so that the cameras were 1.8 m apart and 0.8 m from the bottom of the frame with their optical axes offset horizontally by approximately 90°. The camera platform was connected to a recording station on shore via a 300-m cable assembly consisting of two coaxial video cables (RG59U) that transmitted the video signals to video cassette recorders on shore and a 14-gauge power cable that carried electricity from a 1200-W generator on shore to the lights on the camera platform. Once the fishing gear was deployed, the camera platform was lowered into the water next to the gear and the cable assembly was unwound back to shore. Images were recorded on videotape using two high-density S-VHS recorders (Panasonic AG-6740; Matsushita Electric, Secaucus, N.J.), which allowed 8 h of real-time video (30 frames per second) to be recorded on a single tape. The video recorders' clocks were synchronized during recording to allow analysis of images taken simultaneously by the two cameras.

Fig. 1. Diagram of the camera and light apparatus used to observe walleye (*Sander vitreus*) that encounter gill nets and estimate their sizes.



Videotapes were reviewed to determine the number of fish that encountered, contacted, or become captured by the gear and to estimate the sizes of those fish. We used a video analysis technique developed by Hughes and Kelly (1996) that requires at least two views of the scene and a calibration quadrat, or object of known dimensions, to determine the three-dimensional (3-D) location of objects in the field of view of the cameras. Our calibration quadrat consisted of a 1-m^3 aluminum frame with 10-cm^2 grids on four sides, which was lowered into the field of view of the cameras and oriented so that two of the four sides were perpendicular to the optical axis of each camera. We recorded the images of the calibration quadrat from both cameras for 1 min and then removed the quadrat from the water. We used the methods of Hughes and Kelly (1996), with slight modification, to estimate fish size. Video images were digitized using an IBM-compatible computer with a video capture card. We used NIH Image software, a JAVA program, and two Excel macros to calibrate the video images and calculate 3-D locations

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of a fish's snout and tail locations from the two views. The JAVA program and Excel macros were provided by L.H. Kelly (Bureau of Land Management, Northern Field Office, 1150 University Avenue, Fairbanks, AK 99709-3844, U.S.A., personal communication; available for download at http://aurora.ak.blm.gov/science/).

Walleye observations

To illustrate the methods, we estimated the probability that walleye would be retained after contacting multifilament nylon gill nets. We observed walleye encountering gill nets in Moody Lake using the camera apparatus during open water on five nights in October 1999, 31 nights from late April to October 2000, and 12 nights from May to August 2001. Moody Lake is a small (17 ha), clear lake in central Minnesota with a maximum depth of 3.7 m and a Secchi depth usually exceeding the maximum depth. Moody Lake was used to extensively raise walleye fingerlings in the 1980s, but was later abandoned because of lack of winterkill. The fish community was dominated by walleye surviving from the original stockings. Walleye in Moody Lake were limited in their size range, most being between 270 and 350 mm fork length (FL) in 2000, and exhibited poor condition and slow growth because of lack of forage fish. To increase the size range of fish in Moody Lake, we introduced 22 walleye between 424 and 582 mm total length (TL) in 2000 and 275 walleye between 384 and 636 mm TL in 2001. Walleye introduced in 2000 were from Whitefish Lake and did not differ significantly in their length–girth relationship from Mille Lacs Lake walleye (G. Grant, unpublished data), whereas walleye introduced in 2001 were from Mille Lacs Lake.

We modified standard Minnesota experimental gill nets (Minnesota Department of Natural Resources 1993) to reduce the number of walleye killed outside the field of view of the cameras. Each night we used one 3-m-long panel consisting of 25-, 32-, or 38-mm bar mesh, the three mesh sizes we calculated would be most effective at capturing the size of walleye present in Moody Lake. Each panel was centered on 15.5-m lead and float lines to simulate a longer net because we noticed our standard nets were often set loose and bowed both horizontally and vertically because of wind-induced water currents. We set the gill net in the late afternoon and then lowered the camera apparatus next to the net approximately in the center of the panel. The cameras were inspected by SCUBA diving to ensure that they were close enough to the net and that the net had not been tangled and to remove any vegetation between the cameras and the net. Finally, we set a 3-m-high × 50-m-long, 6-mm bar mesh beach seine perpendicular to the gill net panel with one end anchored between the two cameras to lead fish towards the gill net. Within each year, we set the gill net and cameras in the same general location within Moody Lake. In 1999 and 2000, the gill net and cameras were set in the deepest part of Moody Lake (~3.7 m deep), where there was little vegetation, and the seine used to lead walleye into the gill net did not extend to shore. In 2001, we set the gill net and cameras in vegetation in shallower water (~3 m deep) and extended the lead seine to the shore. Once deployed, the lights were activated and the video recorders were started. The nets and camera apparatus were removed the following morning. We measured the FL and girth of all captured fish and noted the method by which they were captured (tangled or wedged) and the point on the body where the mesh was wedged or tangled.

We estimated the FL of each walleye observed to contact the nets using simultaneous estimates of the fish's snout and tail locations. Each walleye observed to touch the net was defined as a single contact regardless of the number of times it touched the net, as long as it remained in the field of view of the cameras. The snout and tail locations were estimated from still images taken when the snout and tail of the fish were visible from both cameras and when the fish was not flexing its tail or body (i.e., was approximately straight). We attempted to obtain at least three sets of simultaneous images for each fish, with each set separated by at least 1 s. However, in some cases we could only obtain one or two sets of images from each fish, and in some cases the images were separated by less than 1 s. FL was calculated as the straight-line distance between the estimated snout and tail fork locations for each set of images, and length of each fish was estimated as the mean FL calculated from the images rounded to the nearest millimetre. We compared the estimated and actual FL of fish that were retained in the nets to calculate errors in the length estimates.

To correct for bias caused by the smaller girth of walleye in Moody Lake, we converted the estimated FL of Moody Lake walleye into estimated TL of walleye from Mille Lacs Lake with equivalent girths. We developed a FL–girth regression for Moody Lake walleye that were captured by angling or in study nets during 2001, where both girth and FL were measured in millimetres.

$$\ln(\text{girth}) = 0.4545 + 0.7926 \ln(\text{FL}), \quad \text{df} = 44,\ R^2 = 0.85 \tag{1}$$

For Moody Lake walleye (≤380-mm FL) that we observed to contact the nets, we used this FL–girth regression to calculate an estimated girth from either the actual FL of walleye that were captured or the estimated FL for fish that were not retained. We then estimated the TL of walleye in Mille Lacs Lake that would have equivalent girths using a regression provided by R.E. Bruesewitz (Minnesota Department of Natural Resources, 1200 S. Minnesota Avenue, Aitkin, MN 56431, U.S.A., personal communication), where both TL and girth were measured in millimetres.

$$\ln(\text{TL}) = [\ln(\text{girth}) + 1.6678]/1.1662, \quad \text{df} = 677,\ R^2 = 0.98 \tag{2}$$

Because we never captured any Moody Lake walleye >380-mm FL, fish that were longer than 380 mm were assumed to be stocked, and their estimated FL was converted to TL using equations from Carlander (1997).

Retention curve estimation

For each mesh size, we computed the number of walleye in each 25-mm TL size category that contacted the net and (1) swam through the mesh, (2) were blocked by the mesh but not retained, and (3) were retained by the mesh. We also calculated the ratio of TL to mesh perimeter, x_i, for each i =

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1, 2, ..., n walleye observed to contact the nets. We followed Anderson's (1998) assumption that retention probability depended only on the ratio of fish size to mesh size. To understand the relationship between the method of capture and ratio of TL to mesh perimeter, we plotted the proportion of fish that were captured by wedging and tangling in each 0.2-unit-wide x_i category (i.e., $2.0 \le x_i < 2.2$, $2.2 \le x_i < 2.4$, $2.4 \le x_i < 2.6$, etc.).

To better understand the shape of the retention curve (i.e., skewness), we used our data on captured walleye to determine if there were trends between TL–mesh perimeter ratios and the point on the body that the mesh became wedged or tangled. We calculated the mean TL–mesh perimeter ratio for fish that were wedged to their maxillaries, opercula, pectoral fins, pelvic fins, and dorsal fins. We also noted the range of TL–mesh perimeter ratios of walleye captured by tangling.

Comparison with indirect estimates

We used our empirical data to test Anderson's (1998) relative retention curve for Mille Lacs Lake walleye by comparing the deviances for three models: (1) $P(R) = G$, (2) $P(R) = aG$, and (3) $P(R) = aG(lm^{-1})^c$, where $P(R)$ is the probability of retention, G represents Anderson's (1998) relative retention function for Mille Lacs Lake walleye, a is a proportionality constant that controls the amplitude of the retention curve (i.e., fewer than 100% of fish are caught at the optimal TL–mesh perimeter ratio), c is a rotational constant that adjusts the shape of the curve (i.e., the TL–mesh perimeter ratio where retention is maximized), l represents fish total length, and m represents mesh size. We calculated the deviance, D, for model 1 following the formulas of Hosmer and Lemeshow (1989).

$$(3) \qquad D = \sum_{i=1}^{N} d(r_i, \hat{\pi}_i)^2$$

where

$$(4) \qquad d(r_i, \hat{\pi}_i) = -\sqrt{2|\ln(1 - \hat{\pi}_i)|}$$

when $r_i = 0$, and

$$(5) \qquad d(r_i, \hat{\pi}_i) = \sqrt{2|\ln(\hat{\pi}_i)|}$$

when $r_i = 1$ and where $\hat{\pi}_i$ is the predicted retention probability from Anderson's (1998) retention function (G) for Mille Lacs Lake walleye based on x_i. Estimates of parameters a and c in models 2 and 3, as well as deviance values for models 2 and 3, were calculated by maximum likelihood estimation using the General Linear Model function in S-Plus. We used an analysis of deviance to determine whether additional parameters significantly improved model fit using a χ^2 probability distribution (Hosmer and Lemeshow 1989).

Results

Walleye observations

During 48 net-nights, we observed 153 walleye contact the gill nets, and FL was estimated for 147 of these fish. Of the 147 walleye that contacted the nets for which length could be estimated, 35 were retained, 46 swam through the nets, 29 escaped after being temporarily wedged or tangled, and 37 never became wedged or tangled. The number of walleye that passed through the gill nets and the number retained varied with mesh size (Fig. 2). No walleye swam through the 25-mm mesh, whereas eight walleye swam through the 32-mm mesh and 39 walleye swam through the 38-mm mesh. Thirteen, nineteen, and three walleye were retained in the 25-, 32-, and 38-mm mesh sizes, respectively. Of the 35 walleye that were retained, 27 were wedged in the net and eight were tangled (Fig. 3). The 3-D analysis software produced accurate length estimates; the difference between estimated and actual walleye lengths was not significantly different from zero (t test: $p = 0.218$; actual–estimated: range –12 to 18 mm).

Walleye typically escaped from gill nets by backing out of the mesh and then turning and swimming parallel to or away from the net. Twenty-three of the walleye that were tempo-

Fig. 2. Number of walleye (*Sander vitreus*) in 25-mm size groups that contacted gill nets that passed through (open bars), were blocked (i.e., did not pass through and were not retained; hatched bars), or were retained (solid bars) in (*a*) 25-mm, (*b*) 32-mm, and (*c*) 38-mm bar mesh gill nets. TL, total length.

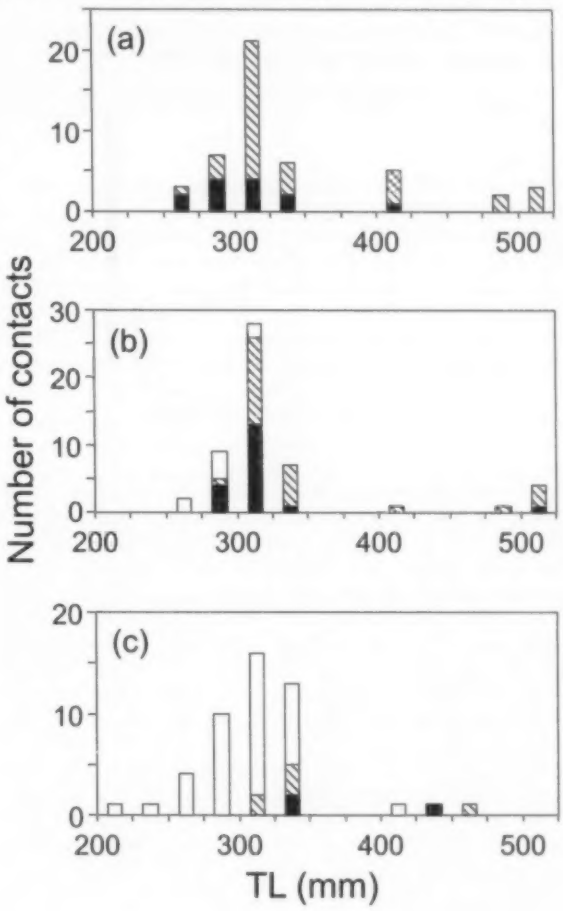

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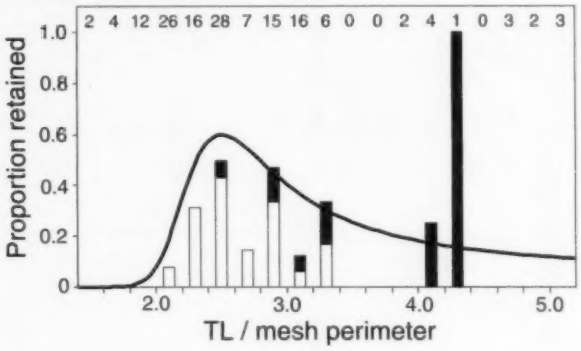
Fig. 3. Proportion of walleye (*Sander vitreus*) in each total length (TL)–mesh perimeter category that were retained after contacting the gill net. The number of contacts observed in each TL–mesh perimeter category is indicated along top of graph. Open bars represent fish that were wedged, whereas solid bars represent fish that were tangled. The solid line represents $0.6G$, where G is the retention probability of Anderson's (1998) gill net selectivity model for Mille Lacs Lake walleye.



rarily retained swam into the mesh but could not swim through. Upon backing out of the mesh, the twine hooked on the maxillary or opercular bones of these fish, and they escaped by turning and swimming away from the net or thrashing their head from side to side to dislodge the twine. Three other fish did not enter the mesh, but were temporarily tangled by their teeth or maxillaries before escaping, whereas two fish turned after contact and became wrapped in the net before escaping. Only one walleye that was temporarily retained was observed to pass through the net upon escaping. Nineteen of the 29 fish that were temporarily retained escaped in less than 1 min, whereas two walleye were retained for >1 h before escaping (maximum 5 h 34 min).

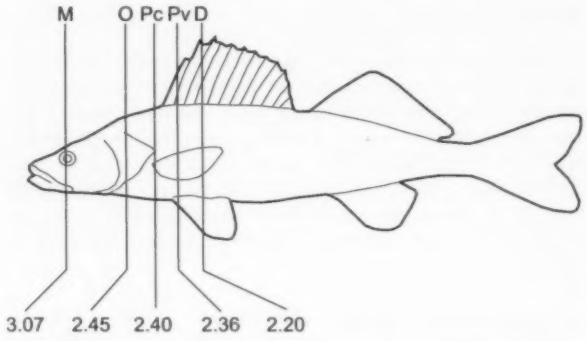
We observed a walleye swim into the net multiple times on 21 occasions; however, each encounter in which the walleye touched the net was considered to be a single contact regardless of the number of times the walleye touched the net. Sixteen walleye that repeatedly swam into the net were never retained, either permanently or temporarily, despite contacting the mesh up to nine times. Three walleye contacted the mesh more than once before being temporarily retained, one walleye contacted the mesh twice before swimming through, and another contacted it twice before being captured.

Retention curve estimation

The retention probability increased rapidly at TL–mesh perimeter ratios between 2.0 and 2.5, then decreased gradually at ratios above 2.5, exhibiting a strong positive skew. A second peak in retention was observed at TL–mesh perimeter ratios between 4 and 4.4 because of larger fish tangling in the net (Fig. 3).

Walleye with larger TL–mesh perimeter ratios were wedged closer to their snout, whereas fish with smaller ratios progressed farther into the mesh before becoming wedged (Fig. 4). The eight walleye that were captured by tangling had TL–mesh perimeter ratios ranging from 2.53 to 4.23 (mean 3.20).

Fig. 4. Mean total length (TL)–mesh perimeter ratios for walleye (*Sander vitreus*) wedged at different points on their body in gill nets. Lines represent the location on the body that the mesh encircled, indicated by the letter above the line. M, maxillary; O, operculum; Pc, pectoral fin; Pv, pelvic fin; D, dorsal fin.



Comparison with indirect estimates

Comparing our empirical data with Anderson's (1998) retention function for Mille Lacs walleye, we found that adding a proportionality constant of 0.60 significantly decreased model deviance, whereas adding a rotational constant did not improve model fit significantly. Our empirical data fit model 2 with a proportionality constant $a = 0.60$ (95% confidence interval, 0.41–0.90) significantly better than model 1 (Table 1). The addition of a rotational constant, c, in model 3 did not significantly reduce the deviance residuals, so we lacked the evidence to refute the shape and modality of Anderson's (1998) relative retention curve (Table 1).

Discussion

The application of underwater video to quantify size selectivity of fishing gear has several advantages over more traditional direct and indirect approaches. Underwater surveillance allows direct estimation of the absolute probability of individual selectivity components, such as the probability that fish encounter, contact, or become retained in the gear. Direct approaches used in the past allow estimation of catchability (i.e., the combination of all selective processes) but not the selectivity occurring at different stages leading up to capture. Indirect approaches can be used to estimate the selectivity occurring at different stages of the capture process, but only on a relative rather than on an absolute scale. Indirectly estimated probabilities inherently depend on model assumptions, whereas the underwater video approach produces empirically derived probabilities that can be used to directly estimate selectivity patterns and validate indirectly derived selectivity models. The technique also allows observation of fish behavior, which leads to a refined understanding of the process of capture in, and escape from, fishing gear. The use of infrared lights allows observation of fish behavior at night without disturbing the fish or altering behavior.

The general approach should be widely applicable to size and species selectivity for a wide variety of fishing gear, including trap nets, trammel nets, baited hooks, and trawls.

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Table 1. Analysis of deviance table for the fit of our binomial data to three models.

Model	Residual df	Residual deviance	Difference		
			df	Deviance	*P*
(1) $P(R) = G$	147	321.868			
(2) $P(R) = aG$	146	138.920	1	182.948	<0.0001
(3) $P(R) = aG(lm^{-1})^c$	145	138.797	1	0.123	0.726

Note: The retention probability $P(R)$ is equal to the following for each model: (1) Anderson's (1998) retention function G; (2) Anderson's retention function with a proportionality constant a; and (3) Anderson's retention function with a proportionality constant a and a rotational constant c; l is fish total length and m is mesh size. Probability values were calculated using a χ^2 probability function.

Hughes and Kelly's (1996) video analysis technique is very flexible in allowing the two cameras to be in any orientation; therefore, the camera platform may be altered based on the size of fish and type of gear being monitored. A camera platform could also be deployed alone to estimate the probability that fish would encounter a gear at a given location.

The primary disadvantages of this technique are that it is limited to environments with high water transparency and only a limited space can be monitored at any time, which may require many nights of observation or high fish densities to collect an adequate sample. Sample size may not be an issue if the entire gear can be monitored (e.g., trap net throat, hook, etc.) and sample sizes can be increased by using multiple camera platforms or increasing deployment time.

By quantifying the absolute retention probability for walleye after contacting gill nets, we were able to estimate the amplitude of the retention curve from Anderson's (1998) gill net selectivity model for Mille Lacs Lake walleye and confirm that it's main mode occurs at TL–mesh perimeter ratios of 2.5. Anderson's (1998) model was generated by assuming the number of walleye of different sizes in Mille Lacs Lake was equal to virtual population analysis estimates, which were based on harvest estimates and tuned with gill net and trawl surveys. Using the virtual population analysis population estimates and catches from annual gill net surveys, Anderson (1998) applied maximum likelihood methods to infer the amplitude and shape of the encounter, contact, and retention selectivity functions. Because the encounter, contact, and retention functions were confounded, the amplitude of the contact and retention functions were normalized to one, suggesting that 100% of walleye that contacted the gill net and were the ideal size for the mesh were retained. We found the probability of retention for walleye in gill nets peaked at 0.60, meaning 40% of walleye that were the ideal size for a given mesh escaped after contacting the net. However, our results confirm that Anderson's (1998) retention function accurately predicted that the optimum TL–mesh perimeter ratio for walleye in gill nets was 2.5.

The shape of Anderson's statistically derived retention curve closely resembled our empirically derived retention data; therefore, we did not have the evidence necessary to refute the shape of Anderson's (1998) retention curve. Because the length distribution of fish observed was limited and the response was binary, the sample size (n = 147) was not adequate to decide whether the shape of the curve should be unimodal or multimodal. Although model 2 has a good fit, the visual impression from Fig. 3 is that the model overestimates $P(R)$ at the left end of the curve, which represents walleye that are wedged in the net.

Thus, modifying Anderson's (1998) retention function to be more realistic only requires adding a proportionality constant of 0.60, indicating the product of the encounter and contact probabilities must be underestimated by a factor of 1.667 (= 0.60^{-1}). Because Anderson's (1998) contact function was also relative (contact probability for the largest mesh size was set to one), it is likely that absolute contact probability is lower than the model predicts, and encounter probability is underestimated by a factor >1.667.

The shape of the retention curve appears to be a function of both walleye morphology and method of capture. Retention due to wedging alone appeared to be unimodal and positively skewed, with the modal TL–mesh perimeter ratio of 2.5 corresponding to walleye that were gilled (i.e., wedged with the twine hooked behind their opercula). The left edge of the retention curve is defined by the threshold of TL–mesh perimeter ratio at which smaller fish can pass through the net, approximately 2.1 for walleye. The ascending limb of the retention curve represents fish with TL–mesh perimeter ratios between 2.1 and 2.5 that can progress into the mesh past their opercula before becoming wedged, whereas the descending limb represents fish that are wedged closer to their snout. Walleye with TL–mesh perimeter ratios >2.5 are typically wedged between their opercula and maxillaries, the maxillary being the most anterior structure that can hook the twine during wedging, preventing fish from backing out of the mesh. The positive skew in retention probability due to wedging may be partly explained by walleye body morphology. The difference between girth at the operculum and maximum girth is less than the difference between girth at the operculum and girth at the maxillary, which results in retention of a narrower size range of fish to the left of the mode and a wider size range to the right of the mode.

Tangling of walleye with larger TL–mesh perimeter ratios caused the retention curve to be positively skewed or possibly bimodal. Our data support Hamley and Regier's (1973) finding that little tangling occurs at TL–mesh perimeter ratios below the optimal value for wedging, presumably because smaller fish eventually swim forward and can pass through the net. Because we observed few walleye with large TL–mesh perimeter ratios contact the nets, it is impossible to determine whether tangling results in a bimodal retention probability curve using our data. Although we stocked larger walleye in Moody Lake, they were much less numerous than the naturalized walleye and were rarely observed. There are also discrepancies in the literature as to whether tangling and wedging result in bimodal selectivity curves for walleye. Hamley and Regier (1973) found that catchability for walleye was bimodal for a given mesh size,

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caused by a combination of unimodal selectivity curves for wedging and tangling, with tangling relatively more important for large mesh sizes. Henderson and Wong (1991) assumed tangling and wedging were dependent processes and did not distinguish between them in their selectivity model for walleye. Walleye selectivity models derived indirectly, where no shape was assumed for the retention curve, have produced both unimodal and bimodal selectivity curves for a given mesh size (Anderson 1998).

Catchability may be bimodal or multimodal for walleye even if retention probability is unimodal, because larger fish may have a higher probability of encountering the nets (Rudstam et al. 1984; Spangler and Collins 1992). When selectivity is computed for a gang of meshes, catchability may be multimodal because of the combination of net sizes and because larger mesh sizes may be harder for fish to detect and avoid (Anderson 1998). Baranov (1914) postulated that all mesh sizes had selectivity curves of the same height, assuming that the thickness of the twine was proportional to mesh size. For Minnesota gill nets, twine size is held constant as mesh size decreases, which should make smaller mesh nets easier to detect and avoid (Hamley 1975).

We did not use our data on encounters and contacts to test the corresponding components of Anderson's (1998) model, although the technique could be applied to any component of selectivity. We assumed that altering the dimensions of the gill net and adding a seine as a lead net biased the number of walleye that encountered the nets. A longer gill net might have led more fish towards the cameras and increased the encounter rate, whereas the lead net probably increased the number of fish that encountered the nets near the cameras. We also assumed that the high transparency of Moody Lake made the nets easier to detect than in more turbid water. However, we assumed that once a walleye contacted a gill net, the overall dimensions of the net and water transparency did not affect the retention probability.

Underwater video has become popular with recreational anglers, but the potential of this tool has not been realized in fisheries research. We believe surveillance of deployed fishing gear to quantify aspects of gear selectivity is one potential use for this tool that can lead to more refined selectivity models and a greater understanding of reaction of fish to gear. We are making further refinements to multiple underwater video camera platforms. Refinements include reducing power requirements by using monochromatic LED (light emitting diode) illuminators, allowing the camera module to be battery-powered and self-contained. Wireless transmission systems are being employed to eliminate cable assemblies, thereby increasing portability and decreasing deployment time. Finally, we are experimenting with camera–light configurations for use in various habitats or with different types of gear, including downward-looking cameras to provide dorsal aspects and improve accuracy of fish size estimates by accounting for flexing during swimming.

Acknowledgements

We are indebted to the late Marie Malskeit for access to Moody Lake and to Lon Kelly and Nick Hughes for providing the 3-D analysis software and instructions. Mike McInerny, Kevin Page, Don Pereira, Rod Pierce, and Jack Wingate reviewed earlier drafts of the manuscript. The paper was improved by the constructive comments of Henry Regier and an anonymous reviewer. This project was funded by the Minnesota Department of Natural Resources and by the Federal Aid in Sportfish Restoration (Dingell-Johnson) Program, Minnesota Project F-26-R, Study 629.

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Effects of predator–prey interactions and adaptive change on sustainable yield

Hiroyuki Matsuda and Peter A. Abrams

Abstract: We explore the effects on population size and yield of different levels of harvesting of a predator in a predator–prey system. We consider the consequences of adaptive change in the predator's foraging time (or effort) and feedback control of fishing effort. The predator may increase in population size with increasing fishing effort, either when the prey is characterized by a positive effect of its own population size on its own growth rate or when the prey is overexploited by the predator. The predator abundance at which the sustainable yield is maximized can be larger than the abundance without fishing. The effort that achieves maximum sustainable yield and the effort that maximizes predator abundance can both be close to the effort at which the stock collapses. Feedback control in the response to predator abundance may fail to achieve the desired abundance of the target stock or its prey even if the fishing effort is well controlled. These results suggest that developing policies for exploiting adaptive predator species in potentially cycling systems cannot be based on the stable single-species models often used in fisheries management.

Résumé : Notre étude examine les effets de diverses intensités de récolte sur la taille et le rendement d'une population de prédateurs dans un système prédateur–proie en prenant en compte les conséquences du changement adaptatif du temps (effort) de recherche de nourriture du prédateur et des contrôles par rétroaction de l'effort de pêche. La taille de la population du prédateur peut s'accroître en fonction de l'effort de pêche, ou bien lorsque la densité de population de la proie a un effet positif sur son propre taux de croissance, ou alors lorsque la proie est surexploitée par le prédateur. L'abondance du prédateur qui correspond au rendement maximum soutenu peut être plus élevée que lorsqu'il n'y a pas de pêche. L'effort de pêche qui résulte en un rendement maximum soutenu et celui qui maximise l'abondance du prédateur peuvent être très prés de celui qui entraîne l'effondrement du stock. Le contrôle par rétroaction dans la réponse à l'abondance du prédateur peut ne pas réussir à maintenir l'abondance visée du stock ciblé et de sa proie, même si l'effort de pêche est bien géré. Nos résultats montrent que la mise au point de politiques pour l'exploitation d'espèces prédatrices adaptatives dans des systèmes soumis à des cycles potentiels ne peut se baser sur les modèles stables monospécifiques souvent utilisés dans la gestion des pêches.

[Traduit par la Rédaction]

Introduction

Many previous models in fisheries management have implicitly assumed that the abundances of biological resources reach a stable equilibrium. These models have also treated growth rates and natural mortality rates as constants and have usually focused on single-species management. Moreover, until recently, there has been relatively little consideration of species interactions in fisheries ecology; such interactions receive little or no coverage in most textbooks (e.g., Clark 1990; Quinn and DeRiso 1999).

Over the past decade, ecologists and managers have increasingly recognized the importance of species interactions, population cycles, and adaptive traits. It has been suggested that permanent fluctuations in abundance may result from interactions between species. Decadal changes in several pelagic (clupeids in the Baltic, Köster et al. 2001) and demersal (Bering Sea ecosystem, Merrick 1997) fishes have been attributed to changes in environmental factors, as well as predation mortality (Collie and Spencer 1994) and competitive interactions (Matsuda et al. 1992; Matsuda and Katsukawa 2002). Simultaneous changes of prey and predator stocks are interpreted as a consequence of either oceanographic change or ecological interactions (Barange 2001).

The possibility of adaptive change in traits that determine the nature of population growth and interactions between species has also received increasing recognition in the fisheries literature. These properties include life history traits and such interaction-related traits as choice of prey, foraging time, and antipredator traits or behaviours. Heino and Godø (2002) reviewed the importance of adaptive changes in traits for the management of exploited resources, and Conover and

Received 21 January 2003. Accepted 19 October 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 16 March 2004.
J17300

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 doi: 10.1139/F03-147 © 2004 NRC Canada

Munch (2002) have recently documented evolutionary change in life history traits in response to a strong artificial selection imposed by different harvesting regimes. Such adaptive changes in traits are expected to interact with population fluctuations. Abrams and Matsuda (1997) and Abrams (2001) showed that adaptive change in traits related to either predation or escape from predators is capable of changing population sizes and driving or preventing cycles in population sizes. One popular ecosystem model, Ecopath-with-Ecosim, incorporates behaviour in an abstract manner by assuming that increased predator density decreases the predator's per capita capture rate of prey (Walters and Kitchell 2001). Although this is a potential consequence of antipredator behaviour (Abrams and Walters 1996), it is not the only possibility.

Finally, the importance of adopting a multispecies perspective, even when harvesting a single species, is increasingly being recognized (Yodzis 2001). The community ecological context is now incorporated into simulation models used in management (Walters et al. 2000; Walters and Kitchell 2001). Abrams and Rowe (1996) and Abrams (2002) showed that changes in the traits of interacting species can greatly alter the expected response of the abundance of a species experiencing increased mortality due to harvesting or other factors.

In spite of the growing literature described above, there has been relatively little analysis of how these interrelated factors of species interaction, population cycles, and adaptive traits affect fisheries management policies in even the simplest models. Here, we take a step towards filling that gap by analyzing a series of models of the simplest system that includes two interacting species, a predator–prey system. Like most predator–prey models, those analyzed here can exhibit sustained cycles. In addition, our models include adaptive change in a trait that determines a predator's foraging rate. Although we will refer to this trait as "foraging time", the models we discuss should apply to a wide range of traits that increase the predator's rate of capturing prey but that also entail some cost. We use an explicit optimization approach to model the change in this trait with respect to predator abundance. We assume that an increasing relationship exists between foraging time and the per capita mortality rates of the predator species due to both natural causes and fishing. A positive relationship between foraging time or effort and mortality due to higher risk of natural mortality has been demonstrated in many species of fish and other organisms (reviewed in Lima 1998). An increase in the risk of mortality from the fishery with increasing activity is probably reasonable for fish that are caught by angling or by stationary nets; see Heino and Godø (2002) for a fuller discussion of the relationship between activity and mortality. We consider cases in which fishing effort is kept constant and fishing effort is changed based on feedback control (Tanaka 1980). Feedback control is a key aspect of adaptive management (Walters 1986).

We will use this predator–prey model to address several questions. We examine how the population size of a harvested predator species changes as the result of increased fishing effort directed at that species. We are also interested in how yield changes as a function of fishing effort. Finally, we ask whether feedback control of the fishing effort stabilizes the system and (or) increases the average yield and stock abundance. These are all important issues in managing a fishery on a predatory species. They are all issues in which single-species models provide simple answers; the stock size should decrease with increased fishing effort, yield should be maximized at an intermediate effort, and feedback control should maintain the species at a single stable equilibrium. Both the two-species food web and the homogeneous population models that we employ are gross simplifications of natural systems. Nevertheless, understanding such simplified systems is a necessary first step both in knowing what features to include and in understanding the behaviour of more complex models.

We combine a general equilibrium analysis of a model having unspecified component functions with numerical results for a model with specific functional forms. The article compares the dynamics of three types of systems characterized by different parameter values of the specific model. System I reflects the assumptions of most previous theory, a stable system with no adaptively variable traits. System II has both the possibility of cycles and adaptive foraging behaviour that changes in response to fishing pressure. This system assumes that foraging activity increases vulnerability to the fishery and that the adjustment in foraging occurs via evolutionary change. The adaptive change of foraging time is stabilizing in this model. System III is a system in which adaptation occurs on a behavioural time scale, and altered fishing effort does not change behaviour on the time scale of interest. The example of system III that we study is one that would not cycle in the absence of adaptive change but could do so when there is adaptive change in the equilibrium foraging time. We examine how systems II and III differ from system I in the relationship of fishing effort to stock size and yield and how they differ in stability.

Methods

A model for harvesting with changes in foraging time and fishing effort

We consider the following predator–prey system with a dynamic foraging-related trait and the possibility of feedback control of fishing effort. The prey, with abundance N, has a per capita growth rate $R(N)$ in the absence of the predator. The predator, with abundance P, captures prey at a per capita rate given by its functional response, $F(C, N)$, which increases with its mean foraging time C and with N. The rate at which C changes is proportional to the slope of the relationship between individual predator fitness, W, and the trait. This relationship depends on three components of fitness: $D(C)$ is the mortality rate of the predator, which increases with foraging time, $B[F(C, N)]$ is the per capita birth rate of the predator, which is an increasing function of its prey intake rate, and E is the scaled fishing effort on the predator. Catch increases with effort with proportionality constant q, implying that qCP is the catch-per-unit-effort (CPUE). If there is feedback control of fishing effort, the target value for CPUE by the fishery is given by s, and the rate at which this target is approached is determined by a scaling factor, $U(C)$. The units are arbitrary in this model but time t is usually measured by year. Maximum foraging time is normal-

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ized to 1. Different units simply rescale the values of both parameters and variables.

These assumptions result in the following equations:

$$(1a) \quad \frac{dN}{dt} = R(N)N - F(C,N)P$$

$$(1b) \quad \frac{dP}{dt} = W(N,P,C)P = \{-D(C) + B[F(C,N)] - qCE\}P$$

$$(1c) \quad \frac{dC}{dt} = V(C)\frac{\partial W}{\partial C} = V(C)\left[-D'(C) + B'\frac{\partial F(C,N)}{\partial C} - qE\right]$$

$$(1d) \quad \frac{dE}{dt} = U(E)(qCP - s) \text{ if } E > 0;$$

$$\frac{dE}{dt} = \text{Max}[0, U(E)(qCP - s)] \text{ if } E = 0$$

Primes denote derivatives, e.g., B' means dB/dF. $V(C)$ is the velocity of adaptive change in the predator's foraging time, which may depend on current foraging time. The fishing effort is constant if $U(C) = 0$. If $U(C) > 0$, the fishing effort changes with the current CPUE; the linear form used here is one of the several forms of feedback control in population management (Tanaka 1980).

The above model assumes that there is adaptive change in foraging time and that more active fish are more easily caught by the fishery. Several authors have suggested that this could produce evolutionary change in the foraging traits of fish, as reviewed by Heino and Godø (2002). Some evidence suggests that catchability may be a function of predator abundance as well (MacCall 1976; Katsukawa and Matsuda 2003). However, these previous studies have not considered the potential change of foraging time, C, with changing stock size, which could produce the appearance of a direct effect of population size on vulnerability. Thus, we adopt the simpler assumption that catchability is proportional to the foraging time alone.

We first consider the change in the foraging time that is brought about by intergenerational evolution. In this case, $V(C)$ should be small relative to 1 because evolution is significantly slower than population dynamics. We also consider behavioural change in foraging time in response to changes in prey abundance. If eq. 1*c* is used as a model of behavioural change, $V(C)$ is probably much larger than 1, making the change in the foraging trait more rapid than population dynamics. However, because behavioural change itself is the product of long-term evolution, it is unlikely that fish can always detect and respond adaptively to the types and levels of fishing that characterize modern fisheries. In fact, some fishing techniques (luring fish into nets using lights) are based on the inability of fish to respond adaptively. Therefore, we later consider a model for behavioural change that differs in form from our evolutionary model (eq. 1*c*) by leaving out the effect of fishing on trait dynamics (see eq. 4 below).

The favoured foraging time C is a compromise between increasing the functional response, F, which increases birth rate, B, and increases in both the natural and fisheries mortality rates, $D(C)$ and qEC. The optimal compromise depends on the shapes of the component functions. Here, we assume that natural mortality, D, increases at a linear or accelerating rate with foraging traits (Abrams 1984). A simple proportionality seems to be the most probable relationship between foraging and vulnerability to a fishery. The birth rate function B is assumed to be a linear or decelerating function of food intake rate, F; $B' > 0$ and $B'' \leq 0$. Constraints on birth rate must eventually cause birth rate to increase less than proportionally with F.

Functional forms and evaluation methods for numerical explorations

For numerical explorations of the general model, we will use the following functional forms:

$$(2a) \quad R(N) = r\left[1 - \left(\frac{N}{K}\right)\right]$$

$$(2b) \quad F(C,N) = \frac{fCN}{1 + hN}$$

$$(2c) \quad B[F(C,N)] = bF(C,N)^m$$

$$(2d) \quad D(C) = \frac{d}{1 - C}$$

where r is the intrinsic rate of prey population increase, K is the carrying capacity of the prey, f is a positive constant that scales the maximum of the predator's functional response to prey, h is the inverse of the half-saturation abundance of the functional response, b is the maximum energy conversion rate from prey to predator, m is the nonnegative exponent representing the nonlinearity of per capita birth rate of the predator per its prey intake rate, and d is the minimal death rate of the predator. The particular form assumed for the death rate function has the convenient property that the equilibrium trait value is independent of the other parameters when $m = 1$. Even when $m = 1$, $C(t)$ varies with the prey abundance and fishing mortality; it is only the equilibrium value that is constant. Most of the qualitative features of the analysis are similar for many other mortality functions that increase at an accelerating rate with C, but these do not result in a constant equilibrium value for C.

Because the stock size may fluctuate, we are interested in the time average of the yield, which is defined as

$$(3) \quad Y = \frac{1}{T}\int_0^T qE(t)C(t)P(t)dt$$

where T is a time interval that is sufficient to produce an accurate average yield. We ignore the possible time and density dependence of the price p and normalize it to 1. We also ignore the economic discounting of the future harvests in calculating the yield by eq. 3.

Results

Constant fishing effort with intergenerational evolution

We first consider a constant fishing effort, i.e., E is constant or $U = 0$ in eq. 1*d*. We examine the effect of increasing fishing effort on the stability of the general system given by eqs. 1*a*–1*d* and the effects of fishing effort on the stock (predator) population size and on the fisheries yield. Let (N^*, P^*, C^*) denote the population sizes of prey and preda-

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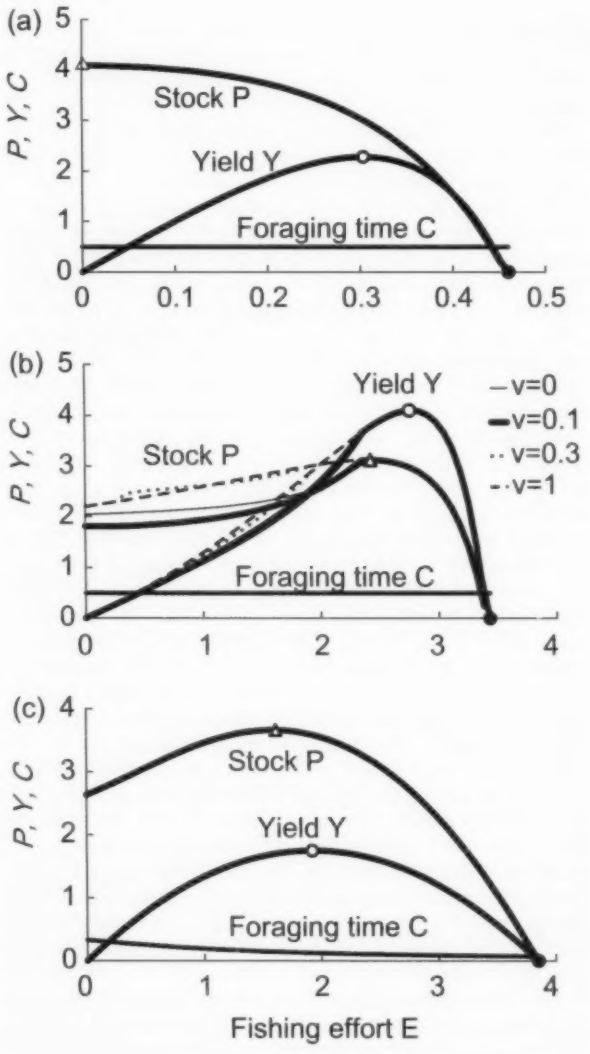
tor and foraging time at the equilibrium. Using linear stability analysis around this equilibrium point and implicit differentiation of the equilibrium conditions, we obtained both the conditions required for a locally stable equilibrium of eqs. 1*a*–1*c* and the expressions for the indirect effects of increased fishing effort (E) on the equilibrium prey abundance (N^*), the equilibrium predator abundance (P^*), and the optimal foraging time (C^*), as shown in Appendix A. The prey abundance always increases with increased E. However, the responses of P^* and C^* to fishing effort are more complicated. It is possible for the equilibrium foraging time to increase or decrease with increased fishing effort. The equilibrium foraging time decreases with increased E if the numerical response, B, saturates strongly as F increases and the equilibrium is locally stable. However, a linear or accelerating numerical response can cause C to increase as prey abundance increases due to heavier fishing pressure on the predator.

One of the more important results from this general model is that adaptive foraging alters the connection between local stability and cases in which P^* increases with increasing E. In the absence of adaptive changes in C, the equilibrium predator abundance can only increase with increasing E in unstable systems. The condition for P^* to increase with an increase in mortality in a model without adaptation (eqs. 1*a* and 1*b*) is exactly the same as the condition for the equilibrium to be unstable; these outcomes both occur when an increase in the prey population, N, has a positive effect on its own growth in the presence of the predator: $(\partial/\partial N)(\mathrm{d}N/\mathrm{d}t) = R + NR' - F'P > 0$. Adaptive foraging, when the initial response of C is to increase when prey abundance increases, can have a strong stabilizing effect. This makes it possible for stability to be maintained even when the immediate effect of increased prey abundance is to increase the prey's growth rate. Higher predator mortality due to greater fishing effort increases both predator and prey abundances. The increase in prey abundance has the effect of reducing the per capita capture rate of prey by predators due to increased predator satiation. This decrease in the effective exploitation rate allows P^* to increase with E, even if the equilibrium C is unaffected by E. A second mechanism allowing an increase in P^* is when the equilibrium foraging time C actually decreases with E. If the prey is initially overexploited (has an abundance lower than that that maximizes its growth rate NR), a lower C increases prey productivity, which allows P^* to increase.

We show several numerical examples of the change in predator population size and yield with increasing fishing effort (Fig. 1). The figure represents three alternative systems that are all based on eqs. 1*a*–1*c* using the functional forms given in eqs. 2*a*–2*d*. The simulations assume that $V(C) = vC$, where v is a small positive constant. The proportionality of adaptive rate to the current foraging time does not affect the position of the equilibrium and slows change in the trait as it becomes small. This form is justified by the fact that variation in C is depleted as it approaches its minimum value of 0.

System I lacks the possibility of adaptive change or population cycles. It is a special case of eqs. 1 and 2 in which foraging time is fixed at its equilibrium value ($C^* = 0.5$, $v = 0$), the death rate parameter d is relatively high, and birth

Fig. 1. Predator abundance, yield, and foraging time as a function of the fishing effort in the systems based on eqs. 1 and 2. Systems I, II, and III (*a*, *b*, *c*, respectively) represent models with different parameter values for the functions in eqs. 2*a*–2*d*. In system I, there is a high mortality rate ($d = 0.6$), moderately large handling time ($h = 0.3$), linear numerical response ($m = 1$), and no adaptive change ($v = 0$). In system II, the predator has a smaller mortality rate ($d = 0.12$), linear numerical response ($m = 1$), and moderate handling time ($h = 0.2$); cases with adaptive rates $v = 0$, 0.1, 0.3, and 1.0 are shown by the thin, thick, dotted, and broken lines, respectively. System III has a concave relationship between the predator birth rate and prey intake rate ($m = 0.5$), no handling time ($h = 0$), and high mortality ($d = 0.6$). Other parameter values for all three systems are $b = 1$, $r = 1$, $K = 20$, and $f = 1$. Circles and triangles represent quantities at which the yield and the stock abundance are maximized, respectively.



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rate is proportional to intake ($m = 1$). As the fishing effort E increases, the equilibrium predator abundance P^* decreases monotonically (Fig. 1*a*), the foraging time C^* does not change, and the product qEC^*P^* (the yield) changes in a unimodal fashion (Fig. 1*a*), implying that the yield is maximized at the intermediate fishing effort given by a small circle on the yield curve.

System II can exhibit unstable dynamics because it allows any value of the predator death rate parameter d. For this system, we consider cases with and without adaptive change in C. Here, we assume a linear function for the per capita birth rate of the predator ($m = 1$). When $v = 0$ (no adaptive change in foraging time), the equilibrium P^* when there is no fishing ($E = 0$) is smaller than P^{**} and is an unstable focus (P^{**} is the maximal equilibrium predator abundance, indicated by a triangle in Fig. 1; N^{**} is the prey abundance corresponding to this point). Both the equilibrium predator stock size P^* and the yield increase as fishing effort E increases; the amplitude of the predator–prey cycle decreases as E increases. If $N^* > N^{**}$, the system reaches the equilibrium and P^* decreases as E increases further (Abrams 2002). Simulations (Abrams et al. (1997) and unpublished report) have shown that the average abundance of the predator, $P(t)$, is smaller than P^* when $N^* < N^{**}$, given eqs. 1*a* and 1*b* with logistic prey growth and a type-2 predator functional response. Because of the unimodal relationship between predator population abundance and fishing effort, predator abundances that are higher than the nonharvested abundance by a particular amount can be produced by two different levels of effort (as shown in Fig. 1*b*). Because equilibrium yield is the product qEC^*P^* and C is constant when $m = 1$ and $v = 0$ in eq. 2*d*, the optimal effort (i.e., the E that maximizes yield of predators) is always larger than the E at which $N^* = N^{**}$ (as shown in system II when $v = 0$) (Fig. 1*b*). In other words, the fishing effort that maximizes the average yield always stabilizes this system even if it is unstable without fishing.

Adaptive change in foraging time can have a strong stabilizing effect when the short-term response of C is to increase in response to an increase in prey abundance. This is generally the case when B is linear and D increases faster than linearly (Abrams 1991), as in system II. In system II, limit cycle dynamics disappear in the presence of sufficiently rapid adaptive change. Even when the equilibrium C^* does not change with fishing effort (as is true for eq. 2*d* when $m = 1$), sufficiently rapid transient changes in the trait value stabilize the equilibrium. The four alternative lines for system II (Fig. 1*b*) show the consequences for average predator abundance and yield of different rates of adaptive change by the predator. The system becomes stable for a prey abundance lower than N^{**} when $v = 0.3$. With a large enough rate of adaptive change (e.g., $v = 1$), the equilibrium is always stable for any fishing effort, and the lines for $v = 1$ represent both the equilibrium and average values of abundance and yield. High enough rates of change effectively make the functional response an accelerating function of prey abundance because foraging time increases rapidly with prey abundance. This has long been known to be stabilizing (e.g., Murdoch and Oaten 1975). Interestingly, the average stock abundance does not exhibit a large change with increased fishing effort over much of the range of possible efforts, and this implies that yield increases approximately proportionally with effort.

System III has a nonlinear birth rate function ($m = 0.5$) and zero handling time (Fig. 1*c*). Together, these assumptions mean that the equilibrium is always stable and that the optimal equilibrium C decreases with increasing fishing effort. The decrease in C implies that predator population size again increases with increasing fishing over the lower part of the range of possible fishing efforts. Here, a reduced C reduces overexploitation and therefore increases P^*. The average predator abundance changes very little with fishing effort, but the average prey abundance increases as fishing effort increases.

Effects of adaptive behaviour in predators

The previous model with a large rate constant, v, may be a good representation of adaptive behaviour, as well as evolution, provided that the predator can respond behaviourally to increased fishing effort. However, as mentioned above, it is likely that many, if not most, fish are unable to detect and respond adaptively via behavioural change to the types and levels of fishing that characterize modern fisheries. We therefore consider a second model for behavioural change that differs from our evolutionary model (eq. 1*c*) in that fishing does not affect the dynamics of C:

$$(4)\qquad \frac{dC}{dt} = V(C)\left[-D'(C) + B'\frac{\partial F(C,N)}{\partial C}\right]$$

Because the predator does not vary its foraging adaptively in response to fishing, the effect of adaptive change on the stability of the equilibrium point is weakened (as shown in Fig. 2). The relationship between prey and predator abundances and fishing effort differs from those illustrated in Fig. 1. Because the foraging time increases with increased fishing effort, the equilibrium and average stock abundances do not change much until the fishing effort reaches that which maximizes the average yield. A limit cycle occurs even when the adaptive velocity parameter, v, is quite large (see the case of $v = 10$ in Fig. 2; cycles also occur for much larger v).

We show limit cycle trajectories in prey–predator space when $v = 0$ and $v = 0.3$ (Figs. 3*a* and 3*b*, respectively), corresponding to the systems represented in Fig. 1*b* (intergenerational evolution), and $v = 10$ (Fig. 3*c*), corresponding to Fig. 2 (adaptive behaviour). The difference between $v = 0.3$ and $v = 10$ is very small (Fig. 2). The defining characteristic of system III is the decrease in optimal foraging time with increased fishing effort. If case III is changed to have a nonzero handling time (as in system II), its nonlinear birth function is more likely to produce cycles than is the comparable model with a linear birth rate ($m = 1$). The average abundances are identical to the equilibrium abundances if the equilibrium is locally stable (Fig. 3*a*). The equilibrium points for a variety of fishing efforts make a parabola that is the isocline satisfying $dN/dt = 0$ in eq. 1*a* with functions 2*a* and 2*b*) (as shown in Figs. 3*a* and 3*b*). The equilibrium is the intersection of the parabola and the vertical line given by the predator isocline satisfying $dP/dt = 0$ (not shown). The predator isocline moves to the right as the fishing effort in-

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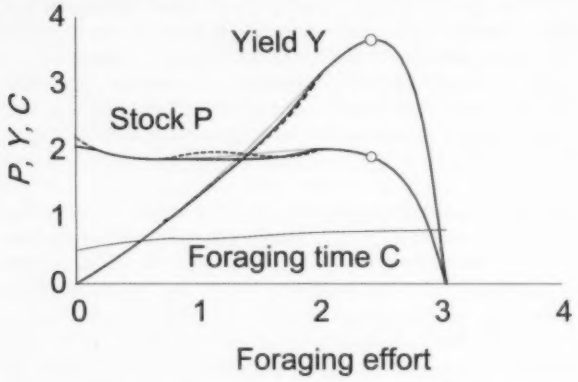
Fig. 2. Predator abundance, yield, and foraging time as a function of the fishing effort in the system consisting of eqs. 1*a*, 1*b*, and 4 when $m = 1$. Parameter values are identical to those in Fig. 1*b* (system II). Solid and broken lines represent average values when $v = 0.2$ and 10, respectively. Shaded lines and circles represent equilibrium values and points, respectively, at which the average yield is maximized.



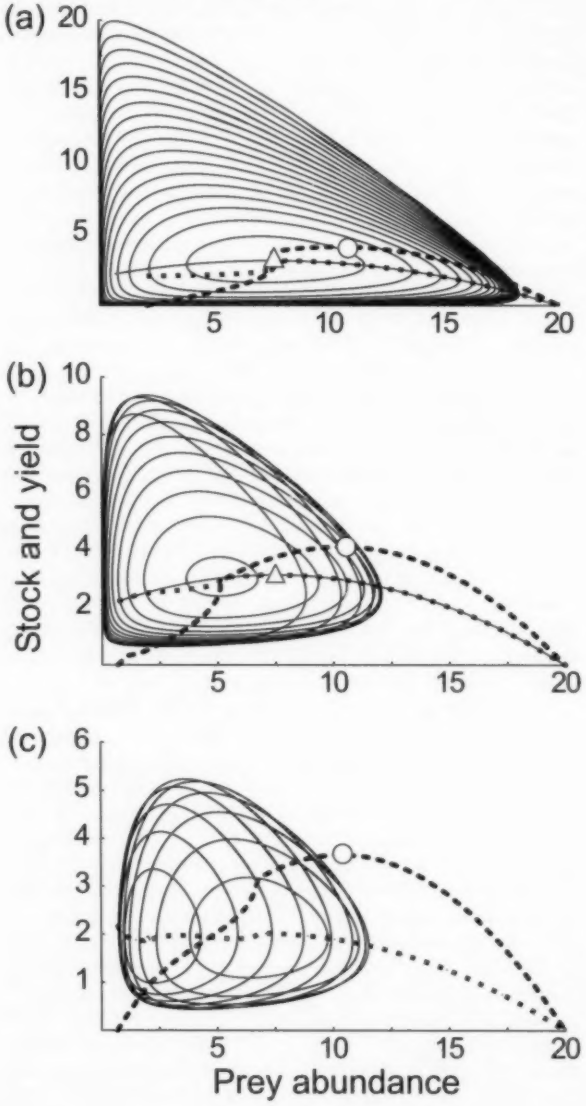
creases. When the equilibrium lies on the left side of the triangle (peak of the parabola), the slope of the parabola is positive, and the equilibrium predator abundance increases with increased fishing effort. Although the average predator abundance is lower than the equilibrium abundance, the average abundance also increases with increased fishing effort. The limit cycles rapidly expand from bottom left (zero effort) to maximum range and then converge to an equilibrium (top) as E increases.

Feedback control of fishing effort

Most fisheries are not characterized by a constant fishing effort. Here, we consider the possibility that fishing effort changes with the abundance or availability of the harvested species. Specifically, we incorporate eq. 1*d*, which means that fishing effort is changed continuously to approach a target yield per unit effort. We assume a proportional constant u for $U(E)$, where u is a positive constant. This reflects a dependence of the maximum rate of change in fishing effort on the current size of the fleet. In this system, fishing effort increases if the CPUE, qCP, is larger than the target quantity s, effort decreases if $qCP < s$, and the magnitude of the rate of change of effort increases with the difference between qCP and s. Tanaka (1980) proposed this feedback management model of fishing effort by analogy to feedback control in technological processes.

We again assume a linear predator birth rate function ($m = 1$ in eq. 2). When the target stock size is greater than the nonharvested equilibrium stock size, there are two equilibria for a given target CPUE, corresponding to equal values of P on either side of P^{**} (denoted by a triangle in Fig. 1). There are two equilibria presented: (N, P, C, E) = (4.5, 2.94, 0.5, 2.1) and (10.5, 2.94, 0.5, 2.9) (Fig. 4*a*). These two equilibria are stable under constant fishing effort ($u = 0$ and $v = 0.5$). However, feedback control in fishing effort ($u = 1$, $s = 1.47$) destabilizes the former equilibrium and the system starting from initial point close to the former reaches the latter equilibrium. The yield increases from the former to the latter

Fig. 3. Limit cycles for variety of fishing efforts when the foraging effort (*a*) does not change ($v = 0$), (*b*) changes by eq. 1*c* ($v = 0.3$), and (*c*) changes by eq. 4 ($v = 10$). The fishing efforts (E) range from 0 to 3.4 (Figs. 3*a* and 3*b*) and from 0 to 3.05 (Fig. 3*c*). Other parameters are $m = 1$, $d = 0.15$, $b = 1$, $h = 0.2$, $K = 20$, and $r = 1$ in eqs. 2*a*–2*d*. Dotted and broken lines represent the average stock and yield, respectively, as a function of the average prey abundance for a variety of fishing efforts. Triangles and circles represent points at which the average stock and yield, respectively, are maximized.



equilibrium as the fishing effort increases and the CPUE is kept constant.

When the birth rate of the predator saturates with increasing prey intake rate ($m < 1$ in eq. 2*c*), the foraging time changes and the CPUE depend on both the stock abundance and the foraging time (vulnerability). Even though the

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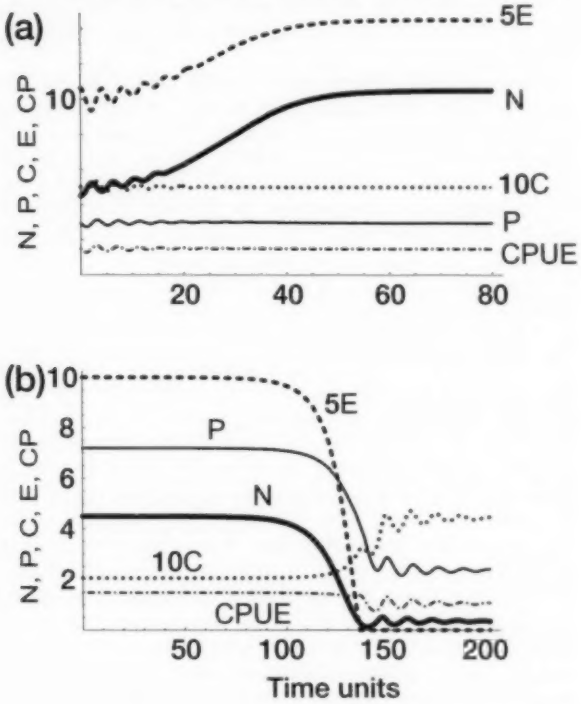
Fig. 4. Temporal changes of prey abundance, $N(t)$, stock abundance, $P(t)$, scaled foraging time, $10C(t)$, scaled fishing effort, $5E(t)$, and CPUE (thick, thin, dotted, dashed, and dotted-dashed lines, respectively) for a system that includes feedback control in fishing effort. (*a*) System II in which parameter values are identical to values in system II in Fig. 1, except that $u = 1$ and $s = qC^*P^* = 1.47$. (*b*) System III in which $m = 0.8$, $d = 0.12$, $b = 1$, $v = 0.5$, $h = 0.2$, $K = 20$, $r = 1$, $u = 1$, and $s = qC^*P^* = 1.47$. The orbit starting from near an equilibrium initially approached this point, but the orbit then converged to the other equilibrium with either (*a*) a larger fishing effort or (*b*) fisheries extinction.



CPUE is kept constant, the stock abundance may change under feedback control. The stock abundance decreased and the foraging time increased, while the CPUE is almost kept constant, and thereafter, the fishery went extinct (Fig. 4*b*). Extinction of the fishery occurs because the stock abundance drops (and stays) below the target abundance. The system starting from near an equilibrium (N^*, P^*, C^*, E) = (4.5, 7.2, 0.204, 2) reached another equilibrium with no fishing and a much lower predator population, (0.35, 2.36, 0.44, 1.19). Both examples show that the abundances of other species or traits of the target species may change under feedback control (Fig. 4); the second example (Fig. 4*b*) shows that this may produce an undesirable outcome even if the fishing effort is well controlled. In both examples, feedback control has consequences that cannot occur under single-species models.

Discussion

The above analysis shows that results from unstable predator–prey models and from both stable and unstable models incorporating adaptive behaviour are quite different from those of the stable models lacking adaptive behaviour that are often used in fisheries management. Here are some of the possibilities observed in the models analyzed above: (*i*) the exploited population may increase in population size with increasing fishing effort and (*ii*) feedback control of fishing effort may cause extinction of the target predator. These results seem to be counterintuitive. Points *i* and *ii* depend on either unstable stock dynamics or adaptive change in trait values. There is no reason to expect that these phenomena no longer occur when the fluctuations are more complicated than limit cycles. Although there are few well-documented cases of predator–prey cycles in fisheries systems (but see Ricker 1997), the dynamic nature of ecosystems is now widely recognized, and a large fraction of the long time series of population abundances show evidence of simple or asynchronous (complicated) cycles or chaos (Kendall et al. 1998).

We explored two types of mechanisms (embodied in systems II and III) that lead to predictions that differ from those of traditional dynamic pool models (system I, see Clark 1990). Under both mechanisms, predator abundance may increase with fishing effort. Although this increase might seem to be advantageous, this situation is potentially dangerous (for both the predator and the fishery) because there will be little indication from the size of the stock when fishing effort approaches the level that will cause collapse of the stock. For example, the fishing effort that maximizes yield (at which the fishing mortality coefficient is referred to as F_{MSY} in standard fisheries terminology, e.g., FAO Fisheries Department 1993) is close to the effort that causes extinction (called F_τ). In the example given by system II, the ratio of F_{MSY} to F_τ is given by the formula

$$(5) \qquad \frac{F_{MSY}}{F_\tau} = \frac{(bf - 4dh)(1 + hK)}{bf(2 + hK)K - 4dh(1 + hK)}$$

It is easy to show that as K becomes very large, this ratio approaches 1; the fishing effort that maximizes yield can become arbitrarily close to the effort that ensures extinction. In system III, the decline in the foraging trait with increasing fishing effort results in a larger difference between the maximum sustainable yield (MSY) fishing effort and the effort that causes extinction. The results for systems II and III suggest that a constant fishing effort (i.e., a constant harvest ratio policy) is often dangerous for stocks that fluctuate because of predator–prey cycles and for stocks that increase with increased fishing effort because of adaptive change in the exploited predator's behaviour. It is important to remember that the increases in stock size under discussion are increases in the equilibrium or long-term average. The initial (transient) response of predator abundance to increased harvest is always decreased population abundance.

We considered a simple linear relationship between the predator's foraging effort and its vulnerability to fisheries, while we assumed a nonlinear relationship between foraging and natural mortality (including that from other predators) in the function D. In reality, a given predator species lives in a complex world that includes its prey and its own predators; the shapes of the trade-offs between foraging and risks from predation have received more attention from theoreticians

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(e.g., Abrams 1984; Matsuda and Namba 1991; Matsuda and Abrams 1994) than from fisheries biologists. Thus, we know relatively little about the shapes of these relationships. Refining the models for a specific system will require such empirical studies. A more detailed model would also include explicit dynamics for the "other predators" rather than assuming a constant risk for a given foraging time characterizing the focal species.

We showed two mechanisms for positive effects of fisheries on the stock: overexploitation by a predator of its prey and adaptive change in foraging effort. Unfortunately, neither one of these mechanisms has received detailed study in an exploited fish population, so far as we know. Overexploitation depends on having an efficient predator or a prey species that suffers little density dependence until its population becomes large. A decrease in foraging time or effort with increased prey abundance is likely when a species has limited reproductive capacity. There is no reason to believe that either of these prerequisites is rare in natural communities or that they will be restricted to any particular taxonomic groups or habitats. Behaviourally determined foraging time or effort has been shown to be sensitive to food and predator abundance in a wide variety of species, including several fish (reviewed in Lima and Dill (1990) and Lima (1998)). Evolutionary change in foraging behaviour is much more difficult to document, but evidence for apparent evolutionary shifts in growth rate (Conover and Munch 2002; reviewed in Heino and Godø 2002) suggests that foraging traits are able to evolve rapidly.

Almost all species have both prey and predators. Single-species models assume that harvesting of a target species affects the stock abundance of only the target species. In contrast, multiple-species models predict that harvesting of a target species may affect the population sizes of other species and may have no effect on or increase the target species. In multiple-species models, increasing fishing effort for a target species may have a positive indirect effect on the stock abundance of that species, as shown above. The possibility of positive indirect effects has been known for general multiple-species models since the work of Yodzis (1988). Yodzis (2001) asserted that complex communities may be characterized by a positive indirect effect between top predators, such as seals and the fish species that they consume. Under the existence of such a positive effect, feedback control destabilizes the coexisting attractors that typically occur in such systems and often makes some other species extinct (H. Matsuda and P.A. Abrams, unpublished data). Although the consequences of exploitation are no doubt different in larger food webs from the consequences for predator–prey systems, there does not seem to be any reason to expect that adaptive behaviour and unstable population dynamics are either less likely to occur or more likely to have intuitive consequences in these more complicated communities. The predator–prey model considered here is only one of a number of possible models that take into account species interactions, adaptive behaviour, and population cycles.

Feedback control in fisheries management is recognized as being a robust and precautionary approach for dealing with uncertainties (Tanaka 1980; Walters 1986). The models considered here suggest that if the system is intrinsically unstable, we may need to intervene in fundamentally different ways if we wish to reduce population fluctuations. However, stability is not always desirable. At least in the predator–prey system that we considered here, instability often allows the maximum sustainable average yield of the prey. If a purpose of feedback control is to avoid outcomes (dynamics) that are not commonly found in natural ecosystems, we should accept the intrinsic instability of nature. Therefore, we need to understand the dynamic properties of both populations and ecologically important characteristics of individuals within those populations. This means that we will often need to monitor not only the population size but also the trait values of the exploited population that determine its interactions with other species.

The models explored here are greatly simplified. We did not consider environmental stochasticity (process errors in population dynamics), age distribution, or spatial structure. We assumed that the stocks could be entirely characterized by their abundance and assumed that mass action terms define predator–prey interactions. If the spatial distribution changes with fishing effort, CPUE does not depend solely on the abundance. Even in two-species models, it is possible that both species adaptively adjust behaviours related to their interaction. Such complications would have to be included if one wanted to determine whether stock size might increase with harvesting in any particular predator–prey system. It is also important to study the transient responses of stocks to different harvesting regimes. The effects of all of these extensions on conclusions about sustainable harvesting are currently largely unknown. However, the possibility of a population increasing with increased harvest has been noted in several other food webs (Abrams 2002), and that paper also showed that this is often true of both transient changes in population size and the equilibrium responses. Yodzis (2001) argued that a key problem in multispecies modeling was the question of what biological details to include in the model. The results presented here argue that adaptive behaviour and the possibility of cycles are both important considerations, and these conclusions are likely to remain true of larger food webs.

Acknowledgements

We thank Drs. T. Katsukawa, N. Kimura, K. Shirakihara, and B. Shuter and anonymous referees for comments on the manuscript. The work was supported by a Strategic Project grant from the Natural Sciences and Engineering Research Council of Canada to P.A.A. and a grant from the Japan Society for Promotion of Science to H.M.

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List of symbols

- B per capita birth rate of the predator (eq. 1*b*)
- b maximum energy conversion rate from prey to predator (eq. 2*c*)
- C foraging time of the predator (eq. 1)
- D death rate of the predator (eq. 1)
- d minimal death rate of the predator (eq. 2*d*)
- E scaled fishing effort on the predator (eq. 1)
- F prey intake rate of the predator (functional response, eq. 1)
- h inverse of the half-saturation abundance of F (eq. 2*b*)
- K carrying capacity of the prey (eq. 2*a*)
- m nonnegative exponent representing the nonlinearity of B (see eq. 2)
- N prey abundance (eq. 1*a*)
- P predator abundance (eq. 1*b*)
- q coefficient related to catchability (qC, eq. 1*b*)
- R per capita growth rate of the prey in the absence of the predator (eq. 1*a*)
- r intrinsic rate of prey population increase (eq. 2*a*)
- s target CPUE under feedback control (eq. 1*d*)
- T time interval sufficient to produce an accurate average yield (eq. 3)
- t time (arbitrary unit, eq. 1)
- U rate at which the fishing effort is changed by feedback control (eq. 1*d*)
- u nonnegative constant ($U(E) = u$ in eq. 1*d*)
- V velocity of adaptive change in the predator's foraging time (eq. 1*c*)
- v nonnegative constant ($V(C) = vC$ in eq. 1*c*)
- W fitness of the predator (eq. 1*b*)
- Y time average of the yield (eq. 3)

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Appendix A. Local stability analysis and indirect effects of fishing on the predator abundance

Applying the Routh-Hurwitz criteria, we obtain the analytical condition for the equilibrium of the system with constant fishing effort given by eqs. 1*a*–1*c* to be locally stable:

$$\text{(A1)}\quad FPVB'F_N\Delta + (R + NR' - PF_N - V\Delta) \times [PFB'F_N - V\Delta(R + NR' - PF_N)] + VPF_C(B'F_{CN} + B''F_CF_N) < 0$$

where $\Delta = D'' - B'F_{CC} - B''F_C^2$. In condition A1, primes denote the derivative of the function with respect to the argument, e.g., R' means dR/dN and B' means dB/dF. Subscripts denote the partial derivative of the function with respect to the argument given by the subscript, i.e., F_N means $\partial F/\partial N$, and consequently, $\partial B/\partial N = B'\partial F/\partial N$. All variables are evaluated at the stable or unstable equilibrium. Given the specific functional forms (eqs. 2*a*–2*d*), Δ is always positive. If eq. A1 is violated, the equilibrium is an unstable focus and the predator and prey fluctuate; in the specific models given by eqs. 2*a*–2*d*, this fluctuation was a limit cycle.

If $V = 0$ (foraging time C is constant), the stability conditions reduce to the single condition $R + NR' - PF_N < 0$, given the assumptions that $B' > 0$ and $F_N > 0$. This inequality is equivalent to the condition that N^* is larger than N^{**} (N^* at which P^* is maximized) because the slope of the isocline, $dN/dt = 0$, in the (N, P) plane is $(R + NR' - PF_N)/F$. If $N^* < N^{**}$, the prey and predator fluctuate, eventually following a limit cycle. When $V > 0$ (the foraging time changes with prey abundance and fishing effort), inequality A1 can be satisfied even if $N^* < N^{**}$. Therefore, adaptive change in foraging time may stabilize the system.

From implicit differentiation of the equilibrium conditions (eqs. 1*a*–1*c*), we obtain a set of simultaneous equations: $(d/dE)(dN/dt) = 0$, $(d/dE)(dP/dt) = 0$, and $(d/dE)(dC/dt) = 0$. Expanding one of these three expressions, $(d/dE)(dP/dt)$ becomes

$$\text{(A2)}\quad \frac{d}{dE}\left(\frac{dP}{dt}\right) = \frac{d}{dE}[W(N, C, E)P] = \frac{\partial W}{\partial E}P + \frac{\partial W}{\partial N}\frac{dN^*}{dE} + \frac{\partial W}{\partial C}\frac{dC^*}{dE} + W\frac{dP^*}{dE} = 0$$

where all derivatives are evaluated at equilibrium. Because $W = 0$ and $\partial W/\partial C = 0$ at equilibrium, $(d/dE)(dP/dt) = [-qC + B'F_N(dN^*/dE)]P = 0$. We obtain $(d/dE)(dN/dt)$ and $(d/dE)(dC/dt)$ in a similar manner and can then solve this system of simultaneous equations to give

$$\text{(A3}a\text{)}\quad \frac{dN^*}{dE} = \frac{qC}{B'F_N}$$

$$\text{(A3}b\text{)}\quad \frac{dP^*}{dE} = \frac{E(R + NR' - PF_N)\Delta - PF_C[qC(B'F_{CN} + B''F_CF_N) - qB'F_N]}{FB'F_N\Delta}$$

$$\text{(A3}c\text{)}\quad \frac{dC^*}{dE} = \frac{qC(B'F_{CN} + B''F_CF_N) - qB'F_N}{B'\Delta}$$

where all variables are evaluated at the equilibrium and Δ is positive if the equilibrium is a stable point or an unstable focus.

Because the per capita birth rate of the predator increases with increased prey intake and the functional response increases with increased prey abundance, $B'F_N$ must be positive. Therefore, from eq. A3*a*, the equilibrium prey abundance always increases with increased fishing effort directed at the predator.

The sign of the predator population's response to increased fishing effort is determined by the two terms in the numerator of the right-hand side of expression A3*b*. The first of these two terms gives the slope of the prey isocline at the equilibrium. Note that this term can only be positive if the prey population is overexploited by the predator, i.e., if $N^* < N^{**}$. Whether or not the entire system is unstable, this first term in the expression for dP^*/dE contributes a positive effect towards the response of the predator population to increased fishing effort. Fishing can increase the stock size of a predator by reducing overexploitation. The second of the two terms in the numerator of expression A3*b* is the response of C^* to E multiplied by a positive quantity (PF_C). Thus, an optimal foraging time that decreases in response to increased fishing effort is a second mechanism by which fishing can increase the population of a predator species in a stable system.

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Transferability of habitat preference criteria for larval European grayling (*Thymallus thymallus*)

M. Nykänen and A. Huusko

Abstract: We examined the transferability of habitat preference criteria for larval European grayling (*Thymallus thymallus*) to two rivers in Finland by testing whether there were significant positive rank correlations between local fish densities (shoals per square metre) and preference indices for depth, velocity, substrate, and vegetation cover or selected combinations. Two sets of preference curves, one obtained from literature for the River Pollon, France, and another for the River Kuusinkijoki, Finland, were tested. All transferability tests for water velocity criteria were successful, correlation coefficients between local fish densities and preference indices ranging from 0.83 to 0.92. Criteria for depth and substrate transferred inconsistently, and criteria for vegetation cover failed to transfer to either target site. Combined indices predicted fish microdistributions inconsistently and they never performed better than the best univariate index for each site. Our results suggest that universal preference criteria for water velocity may exist for larval grayling and that it may be best to use these criteria alone in habitat hydraulic modelling when predicting habitat suitability to larval grayling.

Résumé : Nous avons testé l'application de critères de préférence d'habitat de larves de l'ombre commun (*Thymallus thymallus*) dans deux rivières de Finlande en recherchant l'existence de corrélations de rang positives et significatives entre les densités locales de poissons (bancs par mètre carré) et les indices de préférence de profondeur, de vitesse du courant, de substrat et de couverture végétale, ainsi que certaines combinaisons de ces indices. Deux séries de courbes de préférences ont été utilizées, l'une tirée de la littérature et mise au point sur la Pollon en France et l'autre développée sur la Kuusinkijoki en Finlande. Tous les tests de transférabilité des critères de vitesse du courant ont réussi, avec des coefficients de corrélation entre les densités locales de poissons et les indices de préférence situés entre 0,83 et 0,92. Les critères de préférence de profondeur et de substrat se sont appliqués de façon variable et les critères de préférence de couverture végétale n'ont pu être utilizés dans aucune des deux rivières. Les indices combinés prédisent la microrépartition des poissons de façon irrégulière et ils n'ont pas fonctionné mieux que le meilleur critère unidimensionnel à chacun des sites. Nos résultats indiquent qu'il peut exister des critères d'application universelle de préférence de vitesse du courant chez les larves d'ombres et qu'il est sans doute préférable d'utilizer seulement ces critères dans une modélisation hydraulique de l'habitat quand on veut prédire si un habitat est approprié aux larves d'ombres.

[Traduit par la Rédaction]

Introduction

Biological models describing habitat suitability to fish are perhaps the most important component of physical habitat modelling, a river management methodology where biological data are combined with information on channel structure and hydraulic simulation to predict flow-related changes in fish habitat quality and quantity (Bovee 1986; Parasiewicz and Dunbar 2001). Physical habitat simulation (PHABSIM) is the most widely applied modelling framework, together with other similar microhabitat models (Bovee 1986; Bird 1996; Parasiewicz and Dunbar 2001). In these models, fish are assumed to select microhabitats based on the quality of one or several habitat features, usually depth, velocity, substrate, and cover (Bovee 1986). Suitability of these features to fish is traditionally expressed in the form of univariate habitat utilization (frequency of use) or preference (habitat use related to habitat availability) curves (Bovee 1986; Parasiewicz and Dunbar 2001). Validity of the modelling depends on how accurately these criteria describe and predict the habitat requirements of the target species (Bovee et al. 1998). Since habitat availability and biotic factors, such as predators or competitors, may affect fish habitat selection, use of site-specific criteria has been recommended (Orth 1987; Heggenes 1996). Site-specific criteria are not always available or feasible, however. For example, if a study river deviates significantly from its natural state, criteria from the altered system may not describe the real requirements of the fish but rather conditions they have had to adapt to (Bovee 1986; Bovee et al. 1998). Validation of existing criteria by testing their transferability within and between rivers is therefore needed to strengthen and broaden the utility of habitat hydraulic modelling.

The objective of this study was to examine the transferability of habitat preference criteria for larval European grayling (*Thymallus thymallus*) across river sites. Grayling is threatened in many parts of Europe by regulation and channelization of rivers (Persat 1996), and information on its

Received 8 January 2003. Accepted 30 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 19 March 2004.
J17272

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 doi: 10.1139/F03-156 © 2004 NRC Canada

habitat requirements applicable to management and conservation work are urgently needed. The larvae (total length 15–30 mm) are primarily associated with low-flow areas close to stream margins, and they shift into the main channel once they metamorphose into the juvenile form (e.g., Sempeski and Gaudin 1995*a*, 1995*b*; Nykänen and Huusko 2003). Quantitative habitat preference data for larval grayling presently exist for two rivers (subsequently called source sites), one in France (Sempeski and Gaudin 1995*a*, 1995*c*), and another in Finland (Nykänen and Huusko 2003). We tested the transferability of both criteria sets to two boreal rivers (subsequently called target sites) using a modified habitat suitability overlay approach at a microhabitat scale (Bovee 1986). Our hypothesis was that there would be a positive relationship between local densities of larval grayling and habitat quality predicted by preference indices for depth, velocity, substrate, and vegetation cover if the criteria used were valid. Both univariate indices and different combinations of them were tested to determine if some variables, or variable combinations, were potentially more useful than others in defining habitat suitability for larval grayling.

Methods

Criteria sets and their source sites

We evaluated two sets of univariate habitat preference curves for larval grayling. The first set (depth, mean velocity, and dominant substrate) was obtained from Sempeski and Gaudin (1995*a*, 1995*c*) for the River Pollon, France. The second set (depth, mean velocity, dominant substrate, and percent coverage of vegetation) was developed correspondingly using the preference data (habitat use versus availability) in Nykänen and Huusko (2003) for the River Kuusinkijoki, Finland. As for the River Pollon (Sempeski and Gaudin 1995*c*), the River Kuusinkijoki habitat preferences were determined for intervals of habitat variables (proportional use)/(proportional availability), and these preference values were brought to a common scale by dividing each preference value by the maximum preference value. The most preferred interval thus had a preference of 1.0 and others preferences between 0.0 (unsuitable) and 1.0 (optimal). The Kuusinkijoki curves were smoothed by the distance-weighted least squares smoothing method in SYSTAT 10 for Windows (SPSS Inc. 2000). The River Pollon substrate curve (Sempeski and Gaudin 1995*c*) was modified for the size-classes <2 mm to fit the classification in Nykänen and Huusko (2003): 1, mud or silt: <0.07 mm; 2, sand: 0.07–2 mm; 3, fine gravel: 2–8 mm; 4, coarse gravel: 8–16 mm; 5, fine pebble: 16–32 mm; 6, coarse pebble: 32–64 mm; 7, fine cobble: 64–128 mm; 8, coarse cobble: 128–256 mm; 9, small boulder: 256–512 mm; 10, large boulder: 512–1024 mm; 11, boulders or bedrock >1024 mm.

The River Pollon, the source site for the first criteria set, is a small spring-fed tributary of the River Ain in eastern France. The river has clear water and stable discharge (annual mean 1.1 $m^3 \cdot s^{-1}$) year-round. Fish species present are grayling, brown trout (*Salmo trutta*), chub (*Leuciscus cephalus*), varione (*Leuciscus souffia*), and minnow (*Phoxinus phoxinus*) (Sempeski and Gaudin 1995*b*). Sempeski and Gaudin (1995*a*) collected their habitat preference data for larval grayling in April–June 1993 (water temperature 11.6–14.5 °C) in a 300-m-long reach (approximate location 45°55′N, 05°19′E) that contained both pools and riffles (Sempeski and Gaudin 1995*d*). The fish were observed from riverbank (mean width of river 8.5 m) and characteristics of used habitat were measured along transects in seven river areas occupied by larval grayling (habitat use points $n = 77$). Fish length was visually estimated as 15–30 mm, and larvae that shifted with growth into the main channel (faster and deeper water) were not included in the data (Sempeski and Gaudin 1995*a*).

The River Kuusinkijoki, the source site for the second criteria set, is a medium-sized tributary of the River Oulankajoki in northeastern Finland, about 40 km south from the Arctic Circle. The river has seasonally fluctuating flow. Peak flows (up to 60 $m^3 \cdot s^{-1}$) occur soon after snowmelt in May–June and lowest flows (1–3 $m^3 \cdot s^{-1}$) in winter (annual mean 10 $m^3 \cdot s^{-1}$). Most of the river remains ice covered from mid-November to late April. Fish species present are grayling, brown trout, minnow, whitefish (*Coregonus lavaretus*), northern pike (*Esox lucius*), alpine bullhead (*Cottus poecilopus*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernuus*), roach (*Rutilus rutilus*), burbot (*Lota lota*), and ninespine stickleback (*Pungitius pungitius*). Habitat preference data for larval grayling were collected in June 2000 in a 1-km-long reach (66°11′N, 29°34′E) that contained both pools and riffles (river width 20–150 m) (Nykänen and Huusko 2003). The fish were observed by wading and handnetting within randomly selected areas. Habitat use was measured at the fish points. Nykänen and Huusko (2003) classified larval grayling into three size groups. In the present study, we used the data for the smallest larval group (measured total length 13–25 mm, mean ± SD = 19 ± 2 mm, $n = 126$) (Nykänen and Huusko 2003). These data were collected at a discharge rate of 18.8 $m^3 \cdot s^{-1}$ and water temperature of 11–13 °C. Both the River Pollon and the River Kuusinkijoki habitat preference curves represent the first feeding habitat of larval grayling, before the fish shift into the main channel.

Target sites

We examined the transferability of the River Kuusinkijoki and the River Pollon habitat criteria to two target sites, located in the River Kuusinkijoki and the River Maaninkajoki, respectively. Data were collected at the target sites between 13 (Kuusinkijoki) and 14 (Maaninkajoki) June 2001, when the size of the grayling larvae present in the two rivers corresponded to the range for which the preference criteria were developed. The Kuusinkijoki target site was located 1.5 km upstream from the Kuusinkijoki source site. At the target site, the river was 50 m wide, mainly 0.5–1.0 m deep, and dominated by boulders, very similar to habitat conditions at the source site. We sampled a 30-m-long stretch of the river from the shoreline up to 6 m into the channel. During data collection, discharge rate was 14 $m^3 \cdot s^{-1}$ and water temperature 13.5 °C. Similar to the River Kuusinkijoki, the River Maaninkajoki (66°23′N, 29°03′E) is a tributary of the River Oulankajoki but much smaller, with a discharge of 0.6 $m^3 \cdot s^{-1}$ during the data collection (water temperature 13.5 °C). Species present in the River Maaninkajoki are the same as in the River Kuusinkijoki. At the target site, the river was 6–10 m

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wide, on average 0.3 m deep, and dominated by cobbles and boulders. The area sampled was 30 m long and extended from bank to bank.

Testing for criteria transferability

At the target sites, we located all grayling larvae starting at the downstream end and progressing upstream by wading in a zigzag pattern. After a point had been visually checked for larvae, a hand net was used to sample the same point by a vertical sweep from bottom to surface to ensure no fish were missed in the visual check. The method was considered effective because larval grayling occupy the water column and are not frightened by observers, thus being easily spotted and captured. Individual fish, or centerpoints of shoals, were mapped so that the *X*-coordinate referred to the distance (centimetres) from riverbank and the *Y*-coordinate to the distance from the downstream end of the 30-m long study areas. A random sample of larvae was taken with a hand net at both sites to determine fish lengths. After locating the fish, we determined habitat availability at the target sites by methods similar to those used at the Kuusinkijoki source site (Nykänen and Huusko 2003). Availability was determined along transects placed at 1-m intervals perpendicular to the main current. We took the first measurements at 10 cm distance from the shoreline and the following measurements at every 0.5 m up to 2.0 m distance from the shore, after which measurements were taken at every 1.0 m. Dominant substrate size (particle size most common by area) and vegetation cover (percentage of stream bottom covered by instream vegetation) were determined visually (aided by a viewing box when necessary) in 25 cm × 25 cm quadrants. Water depth and mean velocity (at 60% of total depth from the water surface) were measured at the central points of the quadrants. Altogether, 237 availability points in the River Kuusinkijoki and 328 points in the River Maaninkajoki were sampled. The *X*,*Y*-coordinates of these points were recorded together with the corresponding habitat values.

The transferability of different habitat preference indices, i.e., their ability to predict the spatial distribution of larval grayling at the target sites, was evaluated by a habitat suitability overlay method (Bovee 1986) with modifications similar to those in Beecher et al. (1993) and Guay et al. (2000). First, we converted the depth (Dep), velocity (Vel), substrate (Sub), and vegetation cover (Veg) values at each habitat availability point at the target sites to habitat suitability indices ranging from 0.0 to 1.0 using the River Kuusinkijoki and the River Pollon criteria. Thus, all of the variables, except vegetation cover for which there was no preference index from the River Pollon, received two preference values, one based on the River Kuusinkijoki (K) curves (K[Dep], K[Vel], K[Sub], and K[Veg]) and another based on the River Pollon (P) curves (P[Dep], P[Vel], and P[Sub]). Second, we used simple multiplication (traditional approach; Bovee et al. 1998) to calculate typical combinations of preference indices for each availability point using either the River Kuusinkijoki or the River Pollon indices: K[Dep × Vel × Sub × Veg], K[Dep × Vel × Sub], K[Dep × Vel], P[Dep × Vel × Sub], and P[Dep × Vel]. Third, using the habitat availability data converted to preference values as inputs, contour maps of habitat suitability for grayling larvae were constructed with the aid of the linear interpolation method of kriging in Surfer 7 for Windows (Golden Software, Inc. 1999). The interpolation grid geometry used consisted of 61 rows (*Y*) and 29 columns (*X*) (1769 nodes) for the river Kuusinkijoki site and 61 rows and 41 columns (2501 nodes) for the River Maaninkajoki site. Habitat suitability was grouped into 10 classes of habitat quality index, each presented on the maps with a different color. Altogether, 12 habitat suitability maps were produced for each test site, seven using the River Kuusinkijoki preference curves (four univariate and three composite indices) and five using the River Pollon curves (three univariate and two composite indices). Fish distribution maps were then overlaid with the maps of habitat suitability and the number of fish observations ("shoals" of one or more fish) in each habitat quality class was counted. Next, we calculated the average fish density (as number of shoals per square metre) in each of these classes by dividing the sum of observations in a habitat suitability class by the total surface area of this class (we expressed fish density as density of shoals instead of density of individuals because we believe that habitat selection by an individual grayling within a shoal may not be independent of the behaviour of other fish within that shoal). Only habitat classes with a total area of more than 1 m^2 (the unit over which fish density was averaged) in the study sites were included in the analyses. Finally, we tested the relationship between fish density and habitat suitability (for the 12 different preference indices) using a Spearman rank correlation test. The rank correlation test was used because, according to Bovee (1986), criteria being tested with the habitat suitability overlay method are valid only if fish density increases (ranks higher) systematically (but not necessarily linearly) with habitat quality. Our null hypothesis was that there is no significant relationship between rank of larval density and rank of preferences for depth, mean velocity, substrate, and vegetation cover or their combinations. Our counterhypothesis was that there is a positive relationship (one-sided test). For these tests, habitat quality classes were assigned rank values from 1 to 10 (class 0.0–0.1 = 1, 0.1–0.2 = 2, etc.).

Results

The River Kuusinkijoki habitat preference curves developed using the data in Nykänen and Huusko (2003) had similarities to those of the River Pollon (Sempeski and Gaudin 1995*c*) (Fig. 1). Preferences for water velocity were practically identical in the two rivers with optima at <10 $cm \cdot s^{-1}$. In both the rivers, larval grayling clearly preferred fine substrates (<2 mm), but in the River Kuusinkijoki, coarse particles were also used by the fish. By contrast, the criteria for depth differed notably between the rivers. Whereas depths <10 cm were optimal in Pollon, they were unsuitable (never used) in Kuusinkijoki (optimum at 20–30 cm).

In the Kuusinkijoki target site (total area 155 m^2), 59 fish points (shoals) were recorded, containing 1062 individuals. The median shoal size was eight individuals (mean ± SD = 18 ± 36, maximum 250, 24% of shoals with only one fish). In the Maaninkajoki site (258 m^2), 24 shoals containing 106 individuals were seen. The median shoal size was three individuals (4 ± 5, maximum 20, 29% of shoals with only

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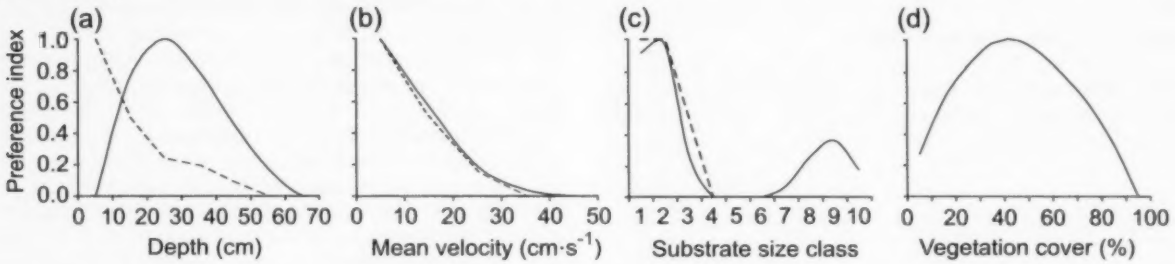
Fig. 1. Habitat preference curves for (*a*) depth, (*b*) mean velocity, (*c*) dominant substrate, and (*d*) vegetation cover for larval European grayling in the River Kuusinkijoki, Finland (solid lines), and the River Pollon, France (broken lines) (modified from Sempeski and Gaudin 1995*b*).

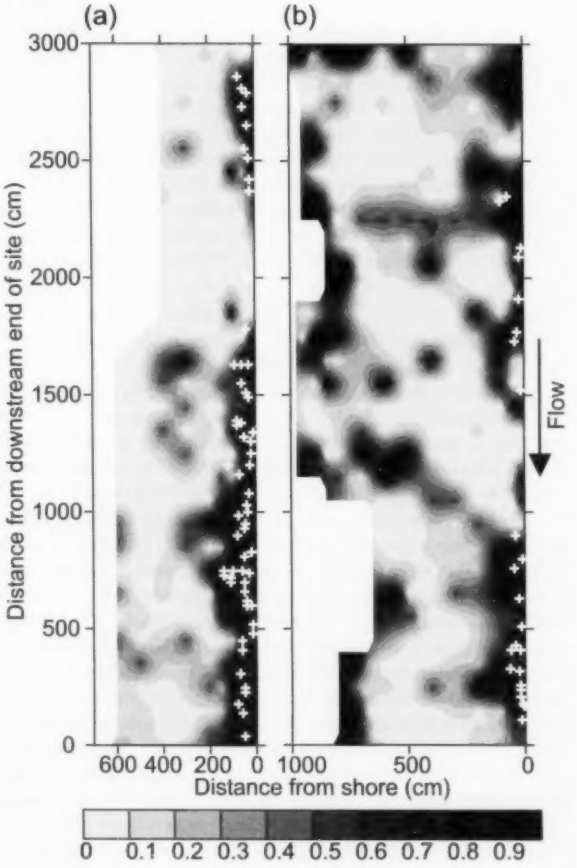


one fish). In the River Kuusinkijoki, the fish were 14–19 mm (minimum–maximum) in total length (16 ± 1 mm, n = 54), and in the River Maaninkajoki length varied from 14 to 16 mm (14 ± 1 mm, n = 44). In both the sites, most fish were observed within 1.0 m of the riverbank. In the Maaninkajoki where both banks were covered, the river formed a bend at the study site, and all of the fish were located near the convex bank (Fig. 2).

The univariate criteria for water velocity transferred well and consistently between the source (the River Pollon and the River Kuusinkijoki) and target sites (the River Kuusinkijoki and the River Maaninkajoki). Criteria for depth and substrate transferred inconsistently, and the criteria for vegetation cover failed to transfer to either of the target sites (Table 1; Figs. 3 and 4). The River Kuusinkijoki univariate preference indices, except vegetation, predicted correctly the distribution of larval grayling in the River Kuusinkijoki target site, i.e., fish density increased with habitat quality (Fig. 3). The larvae clearly avoided areas with depth or velocity preferences <0.5. The selection was even stricter for substrate (although the rank correlation test failed, r_s = –0.273); almost without exception, the fish were found in the optimal habitat (preference index 0.9–1.0). By contrast, in the River Maaninkajoki target site, all other univariate indices of the River Kuusinkijoki but velocity (r_s = 0.825) failed to predict the observed fish distribution (Fig. 3). The composite indices of the River Kuusinkijoki predicted fish distribution at the Kuusinkijoki target site well but not significantly better than depth (r_s = 0.988) or velocity (r_s = 0.918) alone. The best composite index was the product of these two variables (r_s = 0.964). In the River Maaninkajoki, the composite indices of the River Kuusinkijoki all failed to predict the fish distribution (Table 1; Fig. 3).

Of the River Pollon univariate indices, velocity transferred well to the River Kuusinkijoki target site (Fig. 4). Substrate criteria failed the correlation test (r_s = 0.078), but most fish were found in the optimal habitat. The Pollon depth criteria, however, failed to explain fish distribution in the River Kuusinkijoki target site (fish density peaked at an intermediate preference class of 0.3–0.4). At the River Maaninkajoki target site, both the velocity and depth criteria of the River Pollon performed well. The fish clearly avoided areas with preferences <0.5 and the fish density correlated positively with habitat quality (r_s = 0.976 for depth, r_s = 0.914 for velocity). On the other hand, the substrate criteria of Pollon failed completely to predict fish distribution in the Maaninkajoki. All of the composite indices of Pollon failed at the

Fig. 2. Example of the maps produced to determine the utility of habitat preferences to predict distributions of European grayling larvae in (*a*) the River Kuusinkijoki and (*b*) the River Maaninkajoki target sites. The shades of gray indicate habitat quality (preference index 0–1) as determined by the River Kuusinkijoki velocity preference index. Fish locations are marked with white crosses. The maps do not represent the true shapes of the study sites but are justified to the riverbank on the right side of the figures.



Kuusinkijoki target site, but the product of velocity and depth predicted fish distribution well at the Maaninkajoki site (r_s = 0.967) (Table 1; Fig. 4). The composite index was

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Table. 1. Rank correlations between habitat quality (as determined by univariate and combined preference indices of the River Kuusinkijoki and the River Pollon) and density of larval European grayling (shoals·m^{-2}) at Kuusinkijoki and Maaninkajoki target sites.

	Target site					
	The River Kuusinkijoki			The River Maaninkajoki		
Source and type of preference index	n	r_s	p	n	r_s	p
The River Kuusinkijoki						
Depth (Dep)	10	0.988	<0.0005	10	–0.760	—
Velocity (Vel)	10	0.918	<0.0005	10	0.825	<0.005
Substrate (Sub)	10	–0.273	—[a]	4	–1.000	—
Vegetation (Veg)	10	–0.612	—	9	–0.201	—
Dep × Vel	10	0.964	<0.0005	9	–0.559	—
Dep × Vel × Sub	9	0.883	<0.0025	3	–1.000	—
Dep × Vel × Sub × Veg	6	0.943	= 0.01	1	—	—
The River Pollon						
Dep	7	0.464	ns	10	0.976	<0.0005
Vel	10	0.903	= 0.0005	10	0.914	<0.0005
Sub	10	0.078	ns[b]	1	—	—
Dep × Vel	6	0.143	ns	10	0.967	<0.0005
Dep × Vel × Sub	5	0.300	ns	1	—	—

Note: n, number of habitat quality classes available for testing; r_s, Spearman rank correlation coefficient; p, one-tailed significance level; ns, not significant ($p > 0.05$).

[a]Test failed but 68% of the fish observations were in optimal habitat; see Fig. 3.

[b]Test failed but 69% of the fish observations were in optimal habitat; see Fig. 4.

not, however, more useful in explaining the fish distribution than the univariate indices from which it was formed.

Habitat availability differed between the source and target sites, possibly partly explaining the results of the transferability tests. The River Maaninkajoki target site was clearly shallower than the River Kuusinkijoki and the River Pollon sites (Fig. 5*a*), whereas a much higher proportion of slow velocities was available at the River Kuusinkijoki source site than at the three other study sites (Fig. 5*b*). In contrast with other sites, fine substrates (<2 mm) were absent at the River Maaninkajoki site and large boulders were dominant at the River Kuusinkijoki target site (Fig. 5*c*). There was also very little vegetation at the River Maaninkajoki site (Fig. 5*d*).

Discussion

The present results on larval grayling indicate that habitat preference criteria for velocity developed in one river can be successfully used to assess habitat quality and distribution of newly hatched grayling in another river. The findings partly support the assumption of PHABSIM and other habitat hydraulic models that fish select their habitat based on their preferences for the characteristics of the physical habitat, usually water depth, velocity, substrate, and some form of cover (Bovee 1986; Parasiewicz and Dunbar 2001). In the standard application of PHABSIM, a composite suitability index, formed as a product of the univariate preference indices, is most often used (Bovee et al. 1998). The relevance of the individual variables is not always tested. Although fish are likely to select their habitat based on concurrent evaluation of several interacting habitat characteristics (Heggenes 1991), it is probable that some habitat characteristics are more important to fish than others (Freeman et al. 1997). Failure to select the correct variables for a composite index may result in erroneous estimates of habitat suitability (Thomas and Bovee 1993). This was evident in our study, where we tested both univariate and combined habitat preference criteria and found only the criteria for water velocity to consistently correlate with fish abundance.

Our study results support the notion of Scott (1985) and Bardonnet et al. (1991) that for newly emerged larval European grayling, the most limiting physical habitat characteristic appears to be water velocity. First, the two velocity preference curves that we tested, one derived from the literature (Sempeski and Gaudin 1995*c*) and one developed using the preference data in Nykänen and Huusko (2003), were virtually identical despite the differences between the source sites (a small stream in France and a medium-sized river in Finland, respectively). Second, the criteria transferred well to both of our target sites in Finland, the River Kuusinkijoki and the River Maaninkajoki, i.e., there was a significant positive correlation between local fish density and habitat suitability within the areas. Finally, the observations by Scott (1985), Bardonnet et al. (1991), and Sempeski and Gaudin (1995*b*) on grayling habitat use are consistent with the now validated velocity preference data. The apparently universal preference for low water velocities (mostly <10 cm·s^{-1}) is evidently predetermined by the low sustainable swimming speed of larval grayling (Scott 1985). Perhaps for the same reason, velocity criteria transferred well between different sites. Fish habitat use may vary with habitat availability or, e.g., the presence of predators and competitors (Orth 1987; Heggenes 1996), but physical capabilities of the animals inevitably set limits to this flexibility.

Unlike velocity, preference criteria for depth, substrate, and vegetation cover either failed to transfer or transferred inconsistently between rivers in the present study. Bovee (1986) suggested that the more similar the source and target streams, the greater the probability that the criteria are transferable. Indeed, the River Kuusinkijoki criteria for depth, ve-

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Fig. 3. Utility of univariate and composite habitat suitability indices, derived from the River Kuusinkijoki source site, for predicting the distribution of European grayling larvae (density of fish shoals) in the River Kuusinkijoki (●) and the River Maaninkajoki (×) target sites. Indices: (*a*) depth (Dep), (*b*) velocity (Vel), (*c*) substrate (Sub), (*d*) vegetation cover (Veg), (*e*) Dep × Vel × Sub × Veg, (*f*) Dep × Vel × Sub, and (*g*) Dep × Vel.

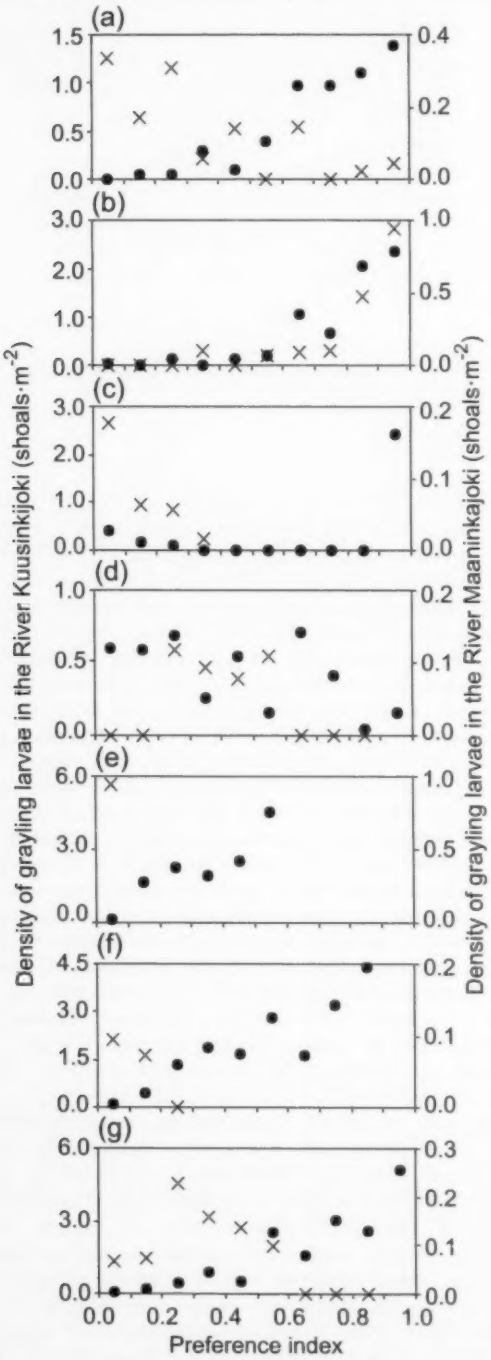
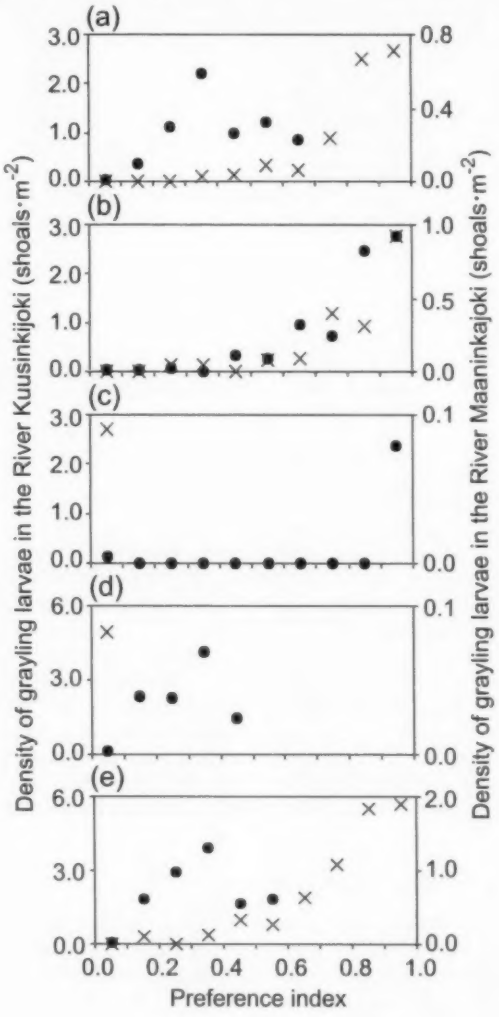


Fig. 4. Utility of univariate and composite habitat suitability indices, derived from the River Pollon source site (Sempeski and Gaudin 1995*b*), for predicting the distribution of European grayling larvae (density of fish shoals) in the River Kuusinkijoki (●) and the River Maaninkajoki (×) target sites. Indices: (*a*) depth (Dep), (*b*) velocity (Vel), (*c*) substrate (Sub), (*d*) Dep × Vel × Sub, and (*e*) Dep × Vel.



locity, and substrate were transferable between the two sites in the river, despite some differences in discharge and habitat availability proportions between the study sites. By contrast, the substrate criteria of Pollon and Kuusinkijoki both failed at Maaninkajoki, at least partly because of differences in substrate availability. Fine particles (<2 mm), preferred at the source sites, were absent in the Maaninkajoki (not available for use). Similarity of habitat availability between source and target sites did not always, however, result in good criteria transference. For example, available depths at the Pollon source site were more similar to available depths at the Kuusinkijoki target site than to those at the much shal-

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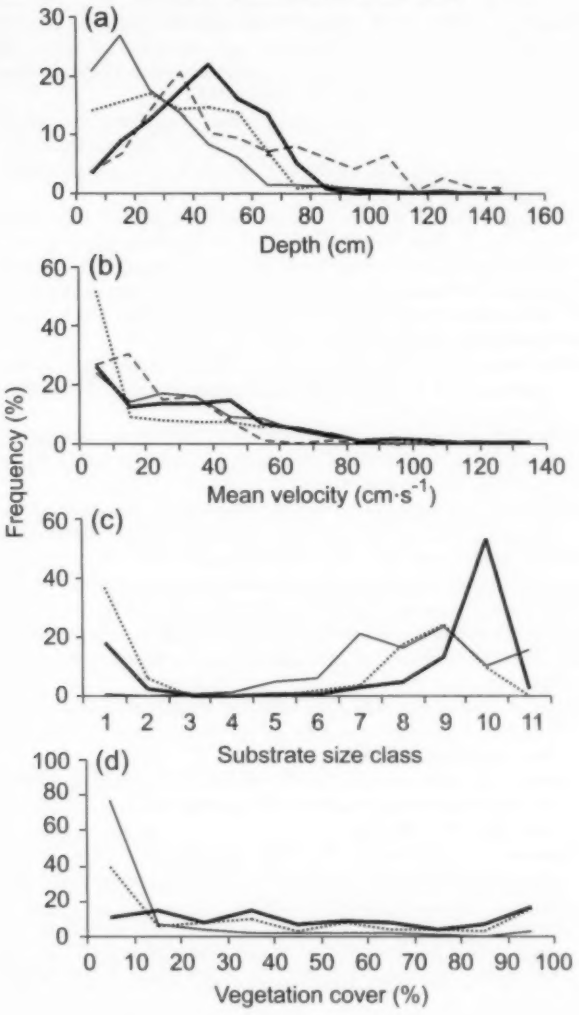
Fig. 5. Availabilities of (*a*) depth, (*b*) mean velocity, (*c*) dominant substrate, and (*d*) vegetation cover in the River Kuusinkijoki source site (dotted line) (modified from Nykänen and Huusko 2003), the River Pollon source site (dashed line) (modified from Sempeski and Gaudin 1995*a*; no data available for substrate or vegetation), the River Kuusinkijoki test site (thick solid line), and the River Maaninkajoki test site (thin solid line).



lower Maaninkajoki site. The Pollon depth criteria, however, transferred well only to the Maaninkajoki site.

Habitat suitability criteria developed elsewhere may fail to transfer to a site also if the criteria do not describe preferred or critical microhabitats (Freeman et al. 1997). According to the substrate criteria of the River Pollon and the River Kuusinkijoki, larval grayling in the River Maaninkajoki were using suboptimal substrates. Whereas use of suboptimal habitats may be possible (as an adaption to available conditions), it is also possible that substrate is not important to larval grayling. Fine substrates are common in low-velocity areas near the riverbanks used by larval grayling. Depending on location, however, these areas can also consist of boulders such as at the Kuusinkijoki source site. Particle size has no obvious function for larval grayling, as the fish rarely hide but occupy the water column where they feed on drifting invertebrates in the midwater (e.g., Scott 1985; Sempeski and Gaudin 1996). Like substrate, depth may also be a secondary variable to water velocity in terms of habitat selection. In the Maaninkajoki site, the marginal areas with suitable velocities were all shallow (mostly <20 cm, gently sloping banks), whereas in Kuusinkijoki, the slow margins were deeper throughout (cut banks). The differences in the depth preference curves and their inconsistent transferability to the target sites may also be due to differences in methods used to collect preference data (Sempeski and Gaudin 1995*a*; Nykänen and Huusko 2003) or differences in habitat availability or biological factors at the source sites. Predators and competitors have been observed to affect use of depth, such that in their presence, young fish increase use of shallow water (Eklöv et al. 1994; Greenberg 1999). We observed no species other than larval grayling during data collection at the target sites. However, their presence and possible influence on the habitat use of the larvae cannot be completely excluded.

PHABSIM and other similar habitat hydraulic models produce an index, the weighted usable area (WUA), of the habitat available to the target species at different flow levels (Stalnaker et al. 1995). A commonly used strategy to validate habitat suitability criteria is to relate WUA produced by PHABSIM and fish biomass (e.g., Orth and Maughan 1982; Bourgeois et al. 1996). However, there are often major uncertainties in both types of data, WUA and fish biomass, that make the results less reliable (Boudreau et al. 1996). The habitat suitability overlay method used avoids many difficulties related to estimating WUA. The overlay method tests the validity of the habitat preference curves, the main component of habitat hydraulic models like PHABSIM, not the methodology itself. The validation does not define a relationship between habitat and biomass but does not deny it either (Boudreau et al. 1996). Differences in global fish densities between rivers (versus local densities) may be better explained by a combination of physical and biological factors (Guay et al. 2000). With various modifications of the habitat suitability overlay method, significant relationships between habitat preferences and fish distribution have been found. Thomas and Bovee (1993) found composite criteria for adult rainbow trout (*Oncorhynchus mykiss*) to be transferable between streams. Guay et al. (2000) found a significant positive correlation between composite on-site criteria and Atlantic salmon (*Salmo salar*) parr density within a river reach. Beecher et al. (1993) tested suitability indices singly and in combination and found a significant rank correlation between steelhead parr density and preferences for velocity alone and for depth and velocity combined but not for depth alone.

In river management, use of microhabitat criteria developed within the study stream is often recommended (e.g., Heggenes 1996). Development of on-site criteria is not, however, always feasible, and criteria applicable across rivers are therefore needed. Our results suggest that universal preference criteria for water velocity may exist for larval grayling and that

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these criteria alone may suffice in habitat hydraulic modelling as an indicator of habitat suitability. In some cases, criteria for depth predicted fish density better than did water velocity. Nevertheless, as depth criteria transferred inconsistently, and they did not improve correlations with habitat suitability and fish density importantly when combined with velocity criteria, their relevance is questionable. Velocities suitable to larval grayling are often found near shore and around instream objects, such as boulders. These small-scale features should be included in models so that the flow patterns generated by them can be distinguished and quantified (Crowder and Diplas 2000).

Acknowledgements

We thank T. Muotka, J.C. Guay, and D. Scruton for their useful comments on earlier versions of the manuscript. The study was partly funded by the Foundation for Research of Natural Resources in Finland and the work of M.N. also by the Biological Interactions Graduate School of Finland.

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The effects of adult length and arrival date on individual reproductive success in wild steelhead trout (*Oncorhynchus mykiss*)

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Abstract: To determine the relative importance of adult size and arrival date for reproductive success in a natural setting, we first genetically determined relationships between all spawning adult steelhead (*Oncorhynchus mykiss*) and juvenile offspring in four brood years and then tested hypothesized relationships between parents' phenotypes and the number and size of their juvenile offspring. Patterns of reproductive success varied among years, but in all cases, a few adults of each sex produced most of the offspring. The number of offspring showed a weak, positive relationship to the mother's size but not to her arrival date. Paternal reproductive success varied considerably but was only weakly associated with size in 1998 and weakly related to arrival date in 2000. In 1997, 1998, and 1999, the offspring of early-spawning females were larger at the end of their first and second summers in the stream; however, in 2000, both arrival date and length were positively related to offspring size. There was no general trend in offspring size in relation to paternal size or arrival date; however, paternal length affected offspring size in 1998 and male arrival date affected offspring size in 2000.

Résumé : Nous cherchons à déterminer l'importance relative de la taille et de la date d'arrivée des adultes de la truite arc-en-ciel anadrome (*Oncorhynchus mykiss*) sur leur succès reproductif dans des conditions naturelles. Nous avons donc déterminé génétiquement les relations entre tous les adultes en fraye et leurs rejetons de quatre cohortes de reproduction et ensuite vérifié l'hypothèse qui veut qu'il y ait des relations entre les phénotypes des adultes et le nombre et la taille de leurs rejetons. Les patterns de succès reproductif varient d'une année à l'autre, mais, dans tous les cas, ce sont quelques adultes des deux sexes qui produisent la majorité des rejetons. Il existe une relation positive, bien que faible, entre le nombre de petits et la taille, mais non la date d'arrivée, de la mère. Le succès reproductif des pères varie considérablement; il n'est que faiblement relié à la taille en 1998 et que faiblement relié à la date d'arrivée en 2000. En 1997, 1998 et 1999, les petits des femelles à reproduction hâtive étaient plus grands à la fin de leurs premier et second étés dans le cours d'eau; en 2000 cependant, la taille des petits était reliée positivement à la fois à la date d'arrivée et à la longueur de la mère. Il n'y a pas de relation constante entre la taille des petits et la taille ou la date d'arrivée du père; néanmoins, la taille des petits était reliée à la longueur du père en 1998 et à sa date d'arrivée en 2000.

[Traduit par la Rédaction]

Introduction

In salmonid fishes, body size is widely believed to determine reproductive success. Larger females produce more numerous and larger eggs (e.g., Beacham and Murray 1993) and are able to bury their eggs deeper (Steen and Quinn 1999), reducing the likelihood of disturbance by the digging of other females (Essington et al. 2000) and protecting them from streambed scour during high-flow events. Large females may also be able to exclude smaller females from the best spawning sites, although prior residence effects may outweigh size (Foote 1990). Larger males can exclude smaller males from access to females through aggressive interactions (Keenleyside and Dupuis 1988; Quinn and Foote 1994). However, dominance is also influenced by prior residence (Foote 1990) and by the level of competition for ripe females, which is a function of date within the spawning period (Quinn et al. 1996).

Salmonids breeding early risk having their redd disturbed by the digging of later-arriving females, and such density-dependent mortality can greatly affect the production of juveniles (Fukushima et al. 1998; Essington et al. 2000). Small males arriving early may gain access to early-arriving ripe females, whereas later in the spawning season, even very large males may be unable to dominate access to females (Dickerson et al. 2002).

Received 31 January 2003. Accepted 21 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 19 March 2004.
J17318

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 doi: 10.1139/F03-158 © 2004 NRC Canada

The size of juveniles may be affected by both maternal size, through correlations with egg size (e.g., Beacham and Murray 1990), and parental spawning date (Einum and Fleming 2000). The progeny of early-spawning adults tend to emerge from the gravel early and may benefit by territory acquisition by prior claim (Chandler and Bjornn 1988; Titus and Mosegaard 1991) and advantages in territorial competition from greater size (Keeley and McPhail 1998) when later fry emerge. Mortality of juveniles can be size selective in freshwater (Smith and Griffith 1994; Quinn and Peterson 1996) and at sea (Healey 1982; Ward et al. 1989), although the strength of selection as well as the direction may vary with rearing environmental conditions (Good et al. 2001). However, relative size within a population may not be maintained as time passes (Herbinger et al. 1995; Heath et al. 1999), depending on food resources (Einum and Fleming 1999), and there may be survival costs to territorial behavior. In addition, early emergence may lead to poor growth if food is not available, and survival rates may be reduced if there is extended exposure to predation (Brännäs 1995).

Almost all studies of selection on size and breeding date in salmonids have been based on behavioral observations, often in experimental settings, and most have measured a surrogate for adult or juvenile fitness such as social dominance or body size rather than actual reproductive success. Population-level studies have produced equivocal findings, including evidence for (Helle 1989; Garant et al. 2001) and against (Holtby and Healey 1986) the hypothesis that larger fish are more productive. Studies using genetic analysis of the parentage of progeny to directly determine reproductive success have almost invariably been conducted in artificial channels or arenas (e.g., Schroder 1981), and progeny have generally been sampled as embryos (e.g., Taggart et al. 2001), precluding consideration of the compensatory processes that operate during later life history stages. Moreover, most studies have neglected variation in female reproductive success and focused on paternity (e.g., Schroder 1981; Jordan and Youngson 1992; Morán et al. 1996). Finally, it is important to determine whether possible interactions between adult size and reproductive timing are additive or multiplicative or whether compensatory processes in natural populations minimize the effects of these factors.

The objective of this study was to determine the relative importance of adult body size and arrival date on reproductive success in salmonids using a wild population of steelhead (*Oncorhynchus mykiss*) as the model system. We predicted that larger females would have larger and more numerous offspring than smaller females and that larger males would have more offspring than smaller males. We further predicted that the progeny of early-arriving adults (male or female) would be larger at the end of their first summer of life and would remain larger in their second summer than the progeny of later breeders.

Methods

Sampling site, collection methods, and genetic analysis

Each spring from 1997 to 2000, the length, sex, and date of upstream migration were recorded for all adult steelhead captured at a permanent fish weir on Snow Creek, Washington. Scales were collected for age estimation, and small pieces of the caudal fin or other tissue were taken for DNA analysis. Our basic assumption was that the weir allowed us to sample the entire spawning population. However, flooding occurred in both 1997 and 1999, enabling adults to pass upstream unsampled. This problem was ameliorated to some extent because a hole was punched in the opercle of adults captured in the upstream trap. Postspawning adults migrating downstream ("kelts") were examined and any that were unmarked were sampled at that time.

Caudal fin tissue from approximately 300 juvenile steelhead was collected annually the first week of October 1997–2000 by single-pass electrofishing in four different sections (each about 100 m long) of Snow Creek. Sampling sites were primarily chosen to cover the upper and lower ends of the range of steelhead rearing habitat with two sections in the middle (see map in Seamons et al. 2004) and secondarily for accessibility. There were no obvious differences in habitat characteristics (e.g., gradient, substrate size) among sampling sites. Immediately above our uppermost sampling site, the gradient appeared steeper with more exposed bedrock. Although juvenile steelhead were found in this habitat, there were substantially fewer compared with the lower reaches encompassed by our sampling sites. All tissue samples were stored in 95% ethanol in 1.5-mL microcentrifuge tubes at room temperature.

DNA extracted from adult and juvenile tissue was used to polymerase chain reaction amplify 12 microsatellite loci (Table 1). All loci were visualized on the MegaBACE 1000 capillary electrophoresis system (Amersham Pharmacia Biotech Limited, Piscataway, N.J.) using fluorescently labeled forward primers for each locus. DNA extraction protocols, polymerase chain reaction conditions, and thermalcycler profiles can be found in Seamons et al. (2004).

Locus characteristics, parentage, and statistical analysis

Adult genetic data from all loci in each sampling year were tested for conformation to Hardy–Weinberg proportions (HWE) with a two-tailed exact test using the Markov Chain method implemented in Genepop 3.1 (dememorization number 1000, batches 100, 1000 iterations per batch; Raymond and Rousset 1995). Significance of probability values was adjusted for multiple tests using sequential Bonferroni correction (Rice 1989). Observed and expected heterozygosities were calculated using GENETIX 4.02 software (Belkhir et al. 2001). The F_{IS}, a measure of inbreeding, was calculated according to Weir and Cockerham (1984) using Genepop 3.1 software (Raymond and Rousset 1995).

A list of potential parents was constructed for each juvenile using the program WHICHPARENTS 1.0 (Will Eichert, Bodega Bay Marine Laboratory, Bodega Bay, Calif.), which compiled a list of all adults that matched one allele at each locus with each juvenile. When compiling the list, we used all 12 loci but allowed three mismatches. The genotypes of adults identified by WHICHPARENTS as potential parents were then directly compared with juvenile genotypes and both adult and juvenile genotypes were checked for errors. Only adults that matched one allele at each locus were assigned as parents. As a conservative measure, because of repeat spawning and the possibility of incomplete adult sampling in some years, all four years of adults were treated as potential parents of all juveniles. In many cases, only one

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Table 1. Allelic variability at 12 microsatellite loci used for parentage assignment in four brood years of steelhead in Snow Creek.

Brood year		Locus											
		Oki23	*Omy1001 UW*	*Omy1004 UW*	*Omy1011 UW*	*Omy1191 UW*	*Omy1212 UW*	*Omy77*	*One108*	*One2*	*Ots107*	*Ots108*	*Ssa85*
1997	N_A	17	12	12	14	18	19	9	11	24	24	16	12
	H_E	0.89	0.87	0.74	0.88	0.92	0.92	0.8	0.88	0.92	0.94	0.91	0.86
	H_O	0.87	0.96	0.84	0.9	1	0.9	0.73	0.87	1	0.87	0.87	0.9
	P_{HWE}	0.75	0.91	0.14	0.62	0.99	0.22	0.13	0.22	0.15	0.37	0.2	0.28
	F_{IS}	0.045	–0.094	–0.119	–0.014	–0.075	0.037	0.096	0.031	–0.073	0.093	0.064	–0.036
1998	N_A	16	12	9	15	18	24	11	14	24	38	19	16
	H_E	0.88	0.86	0.83	0.89	0.9	0.94	0.82	0.88	0.93	0.96	0.91	0.86
	H_O	0.92	0.86	0.85	0.94	0.91	0.96	0.77	0.89	0.98	0.94	0.92	0.89
	P_{HWE}	0.86	0.33	0.39	0.68	0.6	0.53	0.01	0.33	0.46	0.36	0.36	0.82
	F_{IS}	–0.037	0.006	–0.015	–0.055	0.007	–0.012	0.061	0.003	–0.043	0.025	0.003	–0.025
1999	N_A	15	15	12	20	19	11	14	17	29	41	19	18
	H_E	0.87	0.89	0.83	0.91	0.91	0.93	0.84	0.9	0.94	0.93	0.9	0.87
	H_O	0.9	0.96	0.79	0.9	0.88	0.94	0.73	0.85	0.94	0.96	0.87	0.85
	P_{HWE}	0.22	0.42	0.61	0.26	0.76	0.38	0.03	0.01	0.03	0.64	0.44	0.19
	F_{IS}	–0.029	–0.069	0.056	0.012	0.036	–0.001	0.137	0.066	0.011	0	0.052	0.037
2000	N_A	18	17	11	19	22	32	16	17	33	53	22	23
	H_E	0.9	0.88	0.8	0.89	0.9	0.95	0.79	0.9	0.94	0.96	0.91	0.83
	H_O	0.95	0.9	0.78	0.92	0.93	0.96	0.63	0.87	0.99	0.96	0.88	0.83
	P_{HWE}	0.14	0.15	0.75	0.9	0.49	0.18	0.0000[a]	0.02	0.004	0.06	0.001[a]	0.37
	F_{IS}	–0.054	–0.019	0.021	–0.033	–0.038	–0.016	0.209	0.037	–0.052	0.008	0.028	0.012
	Total N_A	20	18	15	20	25	35	17	19	39	58	25	27

Note: Number of alleles per locus (N_A), expected heterozygosity (H_E), observed heterozygosity (H_O), probability after test for goodness of fit to Hardy–Weinberg equilibrium (P_{HWE}), inbreeding coefficient (F_{IS}), and the total number of alleles across all brood years (total N_A) are shown.

[a]Significant at $\alpha = 0.05$.

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parent was assigned to a juvenile. To determine the veracity of our single parental assignment, we calculated the probability of finding an unrelated adult that by chance matched one allele at each locus with a juvenile using the equation

$$(1) \qquad p(\text{random match}) = \prod_{i=1}^{n} 1 - [1 - (pA_i + pB_i)]^2$$

where pA is the probability of matching allele A and pB is the probability of matching allele B based on the parental population allele frequencies multiplied across n loci. If no adults matched one locus at each allele with a juvenile, we assumed that the actual parent(s) had not been sampled. Juveniles not assigned any parents were dropped from subsequent analyses.

To rule out sample processing error as an explanation for our inability to assign at least one parent to all juveniles, we assigned juveniles that had no identified parents to brood years (BY, the year that they were spawned) using age–length histograms made from known-age juveniles. DNA from juveniles and all adults from BYs 1998 and 2000 was reextracted and regenotyped at all loci, and parentage assignment was performed a second time. These two BYs were chosen because they had fewer juveniles with no assigned parents, allowing us to minimize the expense of reprocessing.

To adjust for yearly differences in adult arrival timing and size, all such data were standardized by BY to facilitate combined analyses. Lengths of individual adults were subtracted from the yearly average adult length by sex. Return dates were analyzed as days before or after the median return date by sex within years. Average offspring lengths for each family were calculated and then standardized to the average length of juveniles of that age for that BY. Ages of juveniles were determined from parentage data. About 10% of the adults spawned in more than one year and these individuals were treated as if they were different individuals in the subsequent return year because there was no statistically valid way to compare their performance among years, given the small number of such fish and other confounding factors.

We were unable to record the date when individual fish actually spawned, so we used the date of their arrival at the weir as a surrogate for breeding date. Of the 31 steelhead that returned in 1997, only four were captured in the upstream trap before the high-water event; the rest were captured as downstream migrants after the water had subsided. The actual return date of these fish is unknown, but we assumed that it was during the week when the trap was disabled, so we assigned the midweek date as their arrival date for analysis. Although flooding also occurred in 1999, all adult steelhead sampled in 1999 were caught in the upstream trap, so no estimation of arrival dates was necessary.

Relationships between size and arrival date of parents and the number and size of offspring were first analyzed using a multicovariate weighted least squares general linear model (GLM) (type III, SPSS version 8.0). Covariates consisted of standardized parent length, return date, and year as a fixed factor (for any unaccounted for interannual variation) against number of assigned offspring or average offspring length (within maternal or paternal half-sib families) standardized by the average juvenile length in each BY. Selection was expected to be stabilizing on reproductive timing in salmonids; therefore, the term "return date squared" was included for quadratic analysis of arrival date effects on numbers of offspring for females (Lande and Arnold 1983). Analyses of number of offspring were weighted by yearly sample size because the number of juveniles sampled varied among years. Analyses of offspring size were weighted by the inverse of the family size variance, since families consisted of different numbers of individuals. All possible interaction terms were included in all GLM analyses. If in any test the year or a year interaction term was significant, tests were run as weighted least squares linear regressions (SPSS version 8.0) using individual yearly data. The response variable "number of assigned offspring" was natural log transformed to correct for heteroscedasticity in the data. Whenever individual years were analyzed separately by regression analysis, sequential Bonferroni adjustments for multiple tests were made (Rice 1989).

Undoubtedly, many families of steelhead were missed during our juvenile sampling. Adults not assigned any offspring may have actually produced no offspring or they may have produced offspring that were rearing between our sampling sites. Including adults that produced no offspring would bias analyses, as would excluding adults that produced some offspring. Although it likely affected adult females more than adult males, we chose to exclude all adults that had no assigned offspring from GLM and regression analyses.

Results

Characteristics of adults

From 31 (in 1997) to 139 (in 2000) adult steelhead were captured and sampled at the Snow Creek weir (Table 2). The overall sex ratio was close to 1:1 but varied considerably among years. In 1997, there were nearly twice as many females as males, in 1998 the reverse ratio was observed, and in 1999 and 2000 the sex ratios were nearly 1:1 (Table 2). Body lengths varied considerably: males from 420 to 815 mm and females from 565 to 860 mm. Although the date of first return to Snow Creek varied from December to March, in all years, most steelhead returned in March and April, and the median date of return was in the last week of March in all four years.

Locus characteristics, parentage, and familial relationships

Only two tests out of 48 were out of HWE after sequential Bonferroni corrections (Table 1). Both *Omy77* and *Ots108* showed deviation from HWE ($P < 0.0001$ and $P = 0.001$, respectively). Each was associated with a significant positive F_{IS} value associated with null allele segregation (*Omy77*, $F_{IS} = 0.209$; *Ots108*, $F_{IS} = 0.028$). Average heterozygosity across all 12 loci in our sample was 90% and the probability of exclusion per locus ranged from 0.93 (*Ots107*) to 0.64 (*Omy77* and *Omy1004*). The probability of exclusion using all 12 loci was 0.9999 (CERVUS 2.0; Marshall et al. 1998).

We were able to assign at least one parent to 73% of all juvenile samples and two parents to approximately 40%. The chance of an unrelated adult matching at random the most common possible juvenile genotype (i.e., homozygous for the most frequent allele at each locus in the parent pool)

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Table 2. Number of adult male and female steelhead (N), their size range (SR, mm) and average length (L_{Avg}, mm), and their median arrival date (AD_M).

	Adults										
	Males				Females				Juveniles			
Brood year	N	SR	L_{Avg}	AD_M	N	SR	L_{Avg}	AD_M	N_{0+}	N_{1+}	N_{2+}	N_{NP}
1997	11	420–750	612.7	20 Mar.[a]	20	595–830	692.3	20 Mar.[a]	130	60	1	66
1998	35	600–735	649.6	20 Mar.	18	565–795	638.6	21 Mar.	117	22	2	23
1999	25	400–815	655.6	23 Mar.	27	600–740	658.3	23 Mar.	161	49		134
2000	64	430–785	645.4	23 Mar.	75	565–860	640.0	25 Mar.	245			13
Total	135				140				653	131	3	236

Note: For each brood year, the columns on the right side list the number of juveniles with at least one identified parent in each of three age classes: young-of-the-year (N_{0+}), yearling (N_{1+}), and 2-year-olds (N_{2+}). The rightmost column gives the number of juveniles from each brood year for which no parents were identified (N_{NP}).

[a]Estimated.

for each year was between 1 and 2 in 1000. Thus, in cases where only one adult was assigned, we concluded that that adult was indeed one of the parents. Nearly 27% (294) of all juveniles were not assigned any parents. Based on their body length, 88% of them (258 fish) were apparently from BY 1997 or 1999, both years in which there were floods. Only 23 and 13 juveniles from BYs 1998 and 2000, respectively, had no known parents. Reprocessing of these 36 juveniles and all adults from BYs 1998 and 2000 resulted in six (two from BY 1998 and four from BY 2000) of the juveniles being assigned a single parent and one juvenile from BY 2000 that already had been assigned one parent having a second parent assigned. The genotyping error rate (i.e., total number of incorrect alleles per total number of alleles) based on reprocessed adult samples was 0.6% compared with 3% in reprocessed juveniles.

Twelve adult steelhead returned to spawn in Snow Creek in more than one year (4% of the total), and they produced 54 juvenile offspring. These offspring were assigned to a BY by one of two methods. In 31 cases, a male and a female adult from one BY and only a single adult from another BY (the repeat year of one of the assigned adults) were assigned to a juvenile; thus, we assumed that it was spawned in the BY for which two parents were assigned. In 23 cases, only one parent was assigned (the same individual but two BYs), so the juveniles were assigned to a BY based on juvenile age–length relationships from known-age juveniles.

At least one parent was assigned to 191 juveniles from BY 1997, 141 from BY 1998, 210 from BY 1999, and 245 from BY 2000 (Table 2). Not all adults contributed either young-of-the-year (YOY) or yearling offspring to our samples (Fig. 1). Over 50% of the YOY were the offspring of just 7% (10) of the males and 14% (20) of the females. More than 50% of the yearlings were assigned to only 2% (three) of the total number of males and 6% (nine) of the total number of females. Many families present in the YOY age class were not present in the yearling age class; consequently, the number of adults that failed to produce offspring in our samples increased from 45% to 75% for males and from 28% to nearly 40% for females from YOY to yearlings, respectively. Males were more likely than females to have no offspring assigned to them, and the parents with the most offspring were also males. For both YOY and yearlings, the distributions of offspring among males and females were significantly different (pooled data, two-sample Kolmogorov–Smirnov test, $P = 0.002$ and $P < 0.001$, respectively).

Factors affecting the number of offspring

From 1 to 22 YOY offspring were assigned to individual adult female steelhead, with means ranging from 4.4 offspring per female in 2000 to 9.3 offspring per female in 1998 (Table 3). Standardized variation (σ^2/mean^2) ranged from 0.47 in 1998 to 0.89 in 2000. The range of and mean number of yearling offspring assigned to adult female steelhead also varied little among years (Table 3). Standardized variation ranged from 0.63 in 1999 to 1.06 in 1998.

The GLM that best explained the variation in the number of YOY offspring assigned to females included only the year term ($P = 0.035$) and the length term ($P = 0.05$); however, this model explained very little of the variation ($r^2 = 0.09$). Separate regression analysis for each year also failed to re-

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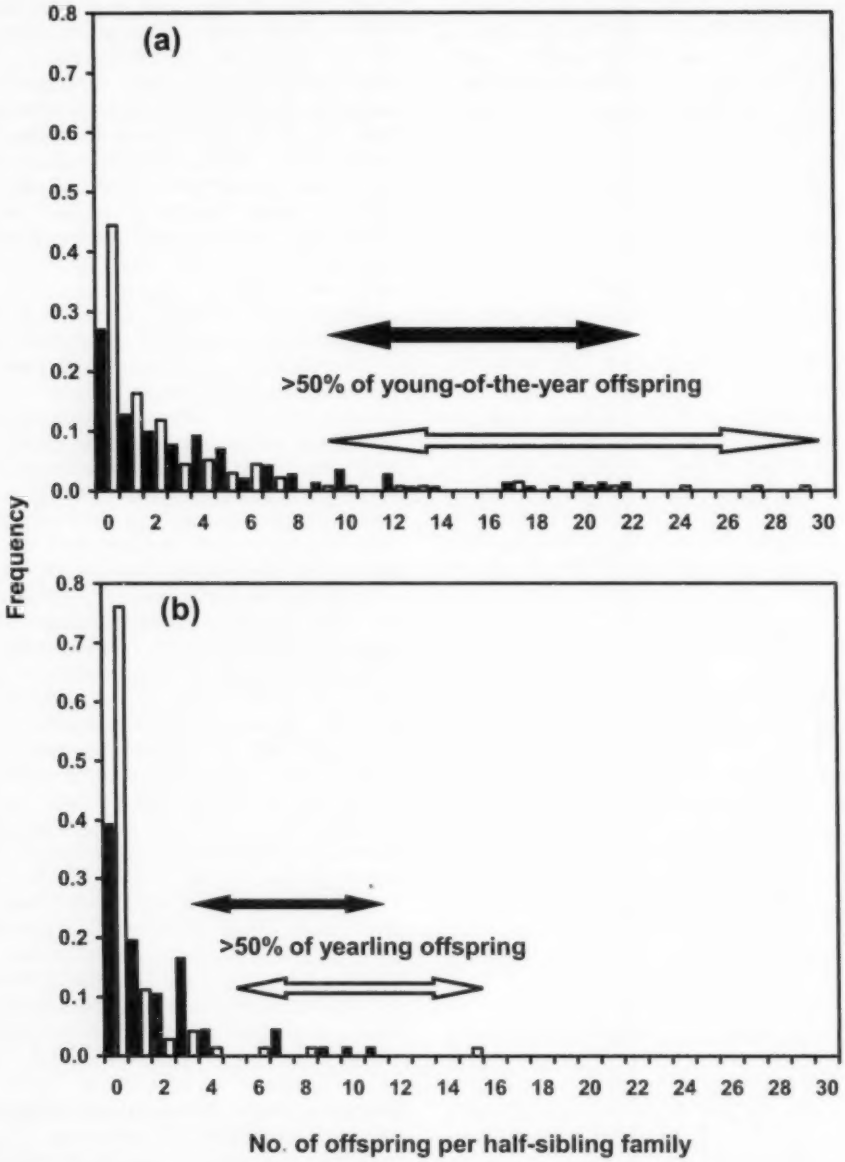
Fig. 1. Frequency histograms showing the frequency of both maternal (solid bars) and paternal (open bars) half-sib steelhead families composed of a certain number of (*a*) young-of-the-year and (*b*) yearling offspring. Arrows encompass the range of low-frequency – large-composition families that add up to more than 50% of the total number of offspring, i.e., most of the juveniles are the offspring of a very few adults.



veal any significant linear relationships (Table 4). However, females that produced five or more YOY offspring were the largest, followed by those that produced three or four offspring, and those that produced one or two were the smallest (Table 5) (one-way ANOVA, $F_{[3,136]} = 5.38$, $P = 0.002$; categories binned to homogenize variance and sample size). Interestingly, the females that produced no detected offspring were intermediate in size, consistent with the idea that this group included both females producing no offspring and some that produced offspring that we did not sample. No GLM successfully explained the number of yearling offspring assigned to adult females, nor did any regression analyses (Table 4). ANOVA comparisons among females categorized by number of yearling offspring revealed no significant differences in mean length among groups (Table 5).

Yearly ranges of YOY offspring assigned to adult male steelhead varied among years from 1–20 in 1997 to 1–29 in 1998 (Table 3), and mean values ranged from 3.9 offspring per male in 2000 to 10.0 in 1997. Standardized variation ranged from 0.40 in 1997 to 2.64 in 1998. Ranges in number of yearling offspring assigned to adult male steelhead also varied among years from 1–3 per male in 1999 to 1–15 in

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Table 3. Summary of observed steelhead parental reproductive success measured as the number of offspring by juvenile age class, parent sex, and brood year with the range, mean, and standardized variance (σ^2/mean^2).

			Brood year			
Juvenile age class	Parent sex		1997	1998	1999	2000
Young-of-the-year	Male	Range	1–20	1–29	1–27	1–21
		Mean	10.0	4.1	6.0	3.9
		σ^2/mean^2	0.40	2.64	1.87	1.32
	Female	Range	1–22	1–22	1–21	1–19
		Mean	6.9	9.3	7.7	4.4
		σ^2/mean^2	0.70	0.47	0.84	0.89
Yearling	Male	Range	1–15	1–4	1–3	
		Mean	5.1	2.3	1.4	
		σ^2/mean^2	0.96	0.44	0.41	
	Female	Range	1–10	1–11	1–9	
		Mean	3.4	3.7	2.6	
		σ^2/mean^2	0.65	1.06	0.63	

Note: No data were available for yearlings from brood year 2000.

1997, and means varied from 1.4 in 1999 to 5.1 in 1997. Standardized variance ranged from 0.41 in 1999 to 0.96 in 1997.

The GLM that best explained variation in number of YOY offspring assigned to adult male steelhead included length and several year, length, and timing interaction terms ($P < 0.02$ all terms) but explained little of the variation ($r^2 = 0.23$). Regression analysis of individual yearly data revealed a significant relationship between length and number of offspring assigned in 1998; no other regression analyses revealed significant relationships (Table 4). One-way ANOVA of mean lengths of males, categorized by number of YOY offspring assigned, was not significant (Table 5), unlike for females. No GLM explained any variation in the number of yearling offspring assigned to adult male steelhead. Linear regression of individual yearly data also yielded no significant results (Table 4), as did one-way ANOVA (Table 5).

Factors affecting the size of offspring

The best GLM for variation in YOY offspring size included adult female length, arrival date, and the year × length interaction term ($P < 0.04$ all terms) and explained a large proportion of the variation ($r^2 = 0.64$). Linear regression analysis revealed that in 1997, 1998, and 1999, arrival date alone explained YOY offspring size (early arrival = large progeny on the sampling date), and in 2000, length and arrival date both explained YOY offspring size variation (Table 4). Plotted against maternal arrival date, a range of about 35 mm in mean length was observed between maternal half-sib families of YOY offspring (Fig. 2).

Yearling offspring size variation was best explained by the GLM that included arrival date and the year × length interaction term ($P < 0.04$ both terms, $r^2 = 0.57$). Linear regression analysis revealed a significant relationship between maternal length and yearling offspring size in 1997 and between maternal arrival date and yearling offspring size in 1998 and 1999 (Table 4). A range of about 27 mm was observed between maternal half-sib families of yearling offspring (Fig. 2).

Only the year and year × arrival date interaction terms explained any variance in the size of YOY offspring attributable to the father (GLM, $P < 0.007$ both terms, $r^2 = 0.33$). Linear regression analysis of individual yearly data showed that length alone predicted offspring size in 1998 and timing alone predicted YOY size in 2000 (Table 4). Neither 1997 nor 1999 showed significant effects of either length or timing. The small number of paternal half-sib families of yearling juveniles (three in 1998 and two in 1999) precluded any statistical analysis of effects of male traits on yearling size.

Discussion

Factors affecting the number of offspring detected

Contrary to predictions, little of the variation in offspring number was explained by female size or arrival date, although smaller females tended to have fewer YOY offspring. As suggested by Holtby and Healey (1986), fitness may be equal among females of various sizes or may be explained by variation in nest site characteristics. In a low-density spawning environment, competition for redd sites may be low (van den Berghe and Gross 1989), so all females may have been able to find suitable spawning sites with little competition or redd site reuse. In addition, scour may not have affected survival of embryos at all, or it may have done so in a manner that was not size selective. Simple models of scour depth predict that redds of smaller females should be more vulnerable than those of larger females in years of high discharge (e.g., Steen and Quinn 1999). However, there is considerable variation in the depth of gravel scour among habitats within even a small area of stream (e.g., Lapointe et al. 2000; Schuett-Hames et al. 2000), and the habitats apparently preferred such as the tailouts of pools are also most vulnerable to scour during floods. If small and large females use different types of habitats, then the differential vulnerability of the sites to scour would result in complex relationships between body size and reproductive success that would vary among years.

A similar study on Atlantic salmon (*Salmo salar*) also failed to find a significant linear relationship between female length or fecundity and number of assigned offspring except when eight large females, assumed to be repeat spawners, were removed from the analysis (Garant et al. 2001). Exclu-

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Table 4. Summary of linear regression analyses for both male and female steelhead parents of both young-of-the-year (YOY) and yearling offspring.

			Male parent		Female parent	
Response variable	Juvenile age class	Brood year	Length	Arrival date	Length	Arrival date
Number	YOY	1997	ns	ns	ns	ns
		1998	$r^2 = 0.13$, $P = 0.06$	ns	ns	ns
		1999	ns	ns	ns	ns
		2000	ns	ns	ns	ns
	Yearling	1997	ns	ns	$r^2 = 0.13$, $P = 0.07$	ns
		1998	ns	ns	ns	ns
		1999	ns	ns	ns	ns
Size	YOY	1997	ns	ns	ns	$r^2 = 0.22$, $P = 0.05$
		1998	$r^2 = 0.54$, $P = 0.036$	ns	ns	$r^2 = 0.58$, $P < 0.05$
		1999	ns	ns	ns	$r^2 = 0.32$, $P = 0.05$
		2000	ns	$r^2 = 0.42$, $P = 0.001$	$r^2 = 0.45$, $P = 0.004$	$r^2 = 0.15$, $P = 0.004$
	Yearling	1997	ns	ns	$r^2 = 0.41$, $P < 0.06$	ns
		1998	ns	ns	ns	$r^2 = 0.92$, $P < 0.06$
		1999	ns	ns	ns	$r^2 = 0.46$, $P < 0.06$

Note: Statistically significant test results are presented; ns signifies a nonsignificant result ($P > 0.10$) based on sequential Bonferroni adjustments for multiple tests. No data were available for yearlings from brood year 2000.

sion of repeat spawners from analysis in our study did not change the significance or nature of the relationship, however. Comparison of the reproductive success of females in their first breeding season with that in subsequent years for iteroparous species such as steelhead and Atlantic salmon is important, but the effort will be hindered by low and variable numbers of repeat spawners and other factors affecting success including but not limited to body size, scour, redd reuse, etc. Previous studies (e.g., van den Berghe and Gross 1989; Fleming and Gross 1994) have emphasized the strong positive effect of female size on many aspects of reproductive success. Despite the logic and empirical evidence for each of these processes, the net result that we observed was much weaker than the sum of all of the individual relationships.

We also found no clear relationship between adult male body size and number of offspring. Large males are observed excluding smaller males from access to ripe females (Quinn and Foote 1994), and it is widely assumed that this behavioral dominance translates to greater reproductive success. Although many males had no assigned offspring, there was no relationship to male length in three of four BYs. However, in one BY, male length was positively correlated with the number of offspring. One of the two largest males seen that year arrived early in the season, stayed late (inferred from the fact that he mated with a female that arrived near the end of the season), and was quite successful (sired 40% of the YOY juveniles), suggesting that size and arrival timing, combined with residence time on the spawning grounds, may influence male reproductive success. This is consistent with correlations with longevity in male pink salmon (*Oncorhynchus gorbuscha*) (Dickerson 2003), although steelhead, unlike Pacific salmon (*Oncorhynchus* spp.), do not necessarily die on the spawning grounds. Instead, male and female steelhead may return to the ocean after spawning. Therefore, male steelhead are expected to stay on the spawning grounds as long as possible to maximize mating success. We were unable to measure residence times for steelhead except for inferences from parentage data in BYs 1997–2000. However, double sampling of steelhead as they migrated up and down past the weir revealed considerable variation in male residence time in BY 2001 (mean = 27 days, $\sigma^2 = 350.5$). Such variation in male residence time on the spawning grounds may have confounded any connection with size.

Clearly, the key to increased reproductive success is not as simple as being big, returning early, and staying late. The operational sex ratio experienced by males may affect their ability to realize their potential reproductive success. In 1998, when our large, early, and steadfast male was successful, we were not able to estimate the number of males upstream of the weir at any point in time, but over the entire spawning season, the sex ratio was highly skewed towards males; therefore, it is likely that at any point in time, there were several males per female. Size may have had a larger effect in this year, whereas in years when more females were available, even small males would have been able to mate. This idea is supported by the fact that in 1997, when the sex ratio was highly skewed towards females, the standardized variation was the lowest, compared with the highest standardized variation in 1998.

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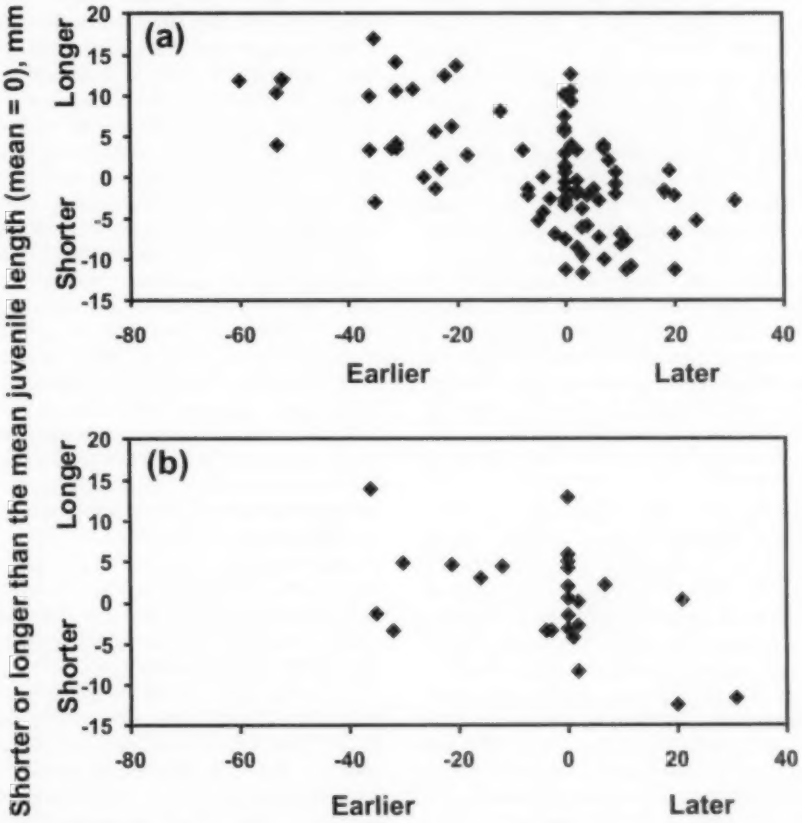
Table 5. Mean lengths (mm) of adult male or female steelhead assigned 0, 1–2, 3–4, or 5+ juvenile offspring (young-of-the-year (YOY) or yearling).

		Male parent		Female parent	
Age class	Number of offspring	*N*	Mean length (±1 SE)	*N*	Mean length (±1 SE)
YOY	0	60	637.5 (±10.9)*a*	38	642.0 (±8.6)*ab*
	1–2	38	641.4 (±7.8)*a*	32	624.8 (±6.0)*a*
	3–4	13	665.0 (±6.8)*a*	24	663.1 (±11.2)*b*
	5+	24	662.5 (±13.0)*a*	46	669.8 (±9.0)*b*
Yearling	0	55	641.5 (±11.0)*a*	14	673.6 (±18.3)*a*
	1–2	10	657.0 (±21.0)*a*	19	655.8 (±10.4)*a*
	3–4	3	676.7 (±26.8)*a*	13	679.6 (±15.1)*a*
	5+	3	661.7 (±46.9)*a*	6	696.7 (±34.9)*a*

Note: Shared letters denote values that are not significantly different from one another (one-way ANOVA, Tamhane's T2 test, $P < 0.04$).

Fig. 2. Relationship between maternal steelhead arrival date and (*a*) young-of-the-year and (*b*) yearling offspring size for all brood years. Maternal arrival date was standardized to the median arrival date in each year. Offspring sizes were standardized to the mean juvenile length per brood year. Relationships were significant at $P < 0.04$ and $P < 0.038$ for young-of-the-year (general linear model, $r^2 = 0.64$) and yearling ($r^2 = 0.57$), respectively.



In addition, timing of breeding is generally believed to have evolved to optimize rearing conditions of offspring. There is a high heritability ($h^2 > 0.8$) for the timing of migration and spawning in salmonids (e.g., Quinn et al. 2000), but success likely varies among years as affected by fish densities and density-independent factors such as flow and

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temperature. We likely did not sample enough BYs to detect the small amount of variation in reproductive success due to spawning date, which would have evolved over many generations.

Finally, there are two possible methodological explanations for the lack of a relationship between parental traits and numbers of offspring: the small fraction of juveniles sampled and their localized spatial distributions. Power to detect significant variation in family size depended on the number of families sampled as well as the number of individuals sampled from each family. The possible number of families depended on the number of adults returning and the mating system (complex patterns of half-sib relationships; Seamons et al. 2004). The number of sampled juveniles ideally would change with the number of spawning adults to have the same chances of sampling a certain number of individuals from a single family, but this was not possible in a natural system. In addition, a representative sample would include sampling a large proportion of rearing habitat. We sampled four sections of Snow Creek, representing a small proportion of the rearing habitat (about 5% by stream length). Undoubtedly, some families were not represented because parents spawned and progeny reared between sampled sections (i.e., no juvenile dispersion). As a qualitative test of the magnitude of juvenile dispersion, we tabulated the sections where members of full-sib families were sampled. Over 30% of the YOY full-sib families were found in two sampling sections (about 1.5 km apart) and 70% were found in only one section. When yearling members of the same full-sib families were added, 5% of full-sib families were found in three sampling sections, about 35% were found in two sampling sections, and 60% were found in one sampling section. These results suggest considerable postemergence dispersal by juveniles, especially in their second year. In spite of this, we likely missed many families, since, because of differential survival, the number of families in existence decreased with time, becoming rare or disappearing altogether, and as yearlings dispersed, they also became much less numerous than the YOY.

In spite of this evidence of juvenile dispersion, we chose to exclude adults assigned no offspring from analyses. Doing so likely underestimated the variance and overestimated the mean reproductive success, since it was likely that some of these adults may have actually reproduced but their offspring were unsampled. Given higher expected variance in reproductive success in males, we would expect this to affect females more than males in our analyses. Indeed, the mean length of females with no assigned offspring was higher than the mean length of those females with one or two offspring and lower than that of females with three or more offspring, whereas there was no difference among male lengths assigned various numbers of offspring. It is possible that some of the larger females that apparently failed to reproduce were actually successful, but their offspring were unsampled. In addition, including males with no assigned offspring improved statistical significance of some linear regressions, whereas doing the same for females did not.

Factors affecting the size of offspring detected

As predicted, large females and those that arrived (and presumably spawned) early had larger YOY and yearling offspring. Indeed, offspring size was more strongly related to the arrival date than the lengths of their parents, suggesting selection for early arrival (and spawning) if offspring size determines survival. However, selection for early spawning will be offset if the redds of early arriving females are disturbed by later-arriving females (Fukushima et al. 1998; Essington et al. 2000); the strength of this density-dependent selection may vary among species, populations, and years. For example, since females of iteroparous species such as steelhead and Atlantic salmon do not guard their nest after completing spawning (Fleming 1998), one might expect more redd reuse than in semelparous species. On the other hand, iteroparous species tend to spawn at lower densities than semelparous species, offsetting this effect. In addition, the link between arrival date and progeny size may be influenced by variation among years in spawning season duration. If all females arrive (and spawn) within a very short time period, as seems to have occurred in 1997, female size may be more important in determining offspring size. Indeed, a significant positive relationship between maternal length and yearling offspring length was seen in 1997.

Surprisingly, male length and arrival date were related to YOY offspring size in one year each: length in 1998 and arrival date in 2000. A correlation between male size and offspring size might occur if large males spawned with large females, but no such correlation was detected (Seamons et al. 2004). Given that offspring size is highly correlated with maternal arrival date, a significant correlation between paternal length and maternal arrival date might also explain the relationship between paternal length and offspring length, but there was no significant correlation between these traits. Additionally, a correlation may exist if there was a high sire effect in additive genetic variation in length. Estimates of sire effects on h^2 for body length are moderate and are generally less than dam effects in hatchery-reared rainbow trout (0.18–0.35) (Gjerde and Gjedrem 1984; Gjerde and Schaeffer 1989). However, naturally reared fish may have higher values of h^2 than fish in captivity; sire effects on h^2 for length, reported by Smoker et al. (1994), were much higher than dam effects in pink salmon reared in their natural environment.

The correlation between male arrival date and offspring in 2000 was likely actually due to the maternal effect of arrival date. Since females determine spawning date and spawning date is correlated with arrival date (e.g., Quinn et al. 2000), males that only spawn shortly after they arrived, as opposed to spawning over the course of the entire season, would acquire the effects of the arrival (and spawning) date of the female with whom they mate. Males in the first three BYs generally spawned many times over the course of the spawning season or spawned at a date not predicted by their arrival date (as inferred from parentage data). However, in 2000, males appeared to spawn only very close to their arrival date.

Parentage assignment

We expected to be able to assign two parents to a great majority of our juvenile samples, and indeed, we were able to assign two adult anadromous steelhead parents to many juveniles. Surprisingly, many juveniles were assigned only one parent, due in part to fertilization of eggs by mature

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male steelhead parr (i.e., unsampled premigratory individuals; Seamons et al. 2004). Even more surprising was the number of juveniles assigned no parents at all. However, the great majority of these juveniles were from years when flooding occurred, 1997 and 1999, suggesting that in these years, many adults spawned upstream of the weir without being sampled. The lack of parental assignment in the few remaining juveniles from BYs 1998 and 2000 may have resulted from one of several processes. These juveniles may have been misassigned by size to BY 1998 or 2000, particularly the 1998 YOY whose size distribution significantly overlapped the distribution of 1997 yearlings. Six juveniles without known parents sampled in 1998 fell within the size overlap range and could therefore actually be from BY 1997. In addition, mutations at one or more loci could have occurred. We were unable to estimate mutation rate, but the rates recently calculated for microsatellite loci in pink salmon by Steinberg et al. (2002) would be insufficient to account for a significant portion of the failure to assign parents. Null allele segregation may also have occurred, although a significant deviation from HWE was found in only two loci in one BY. In many river systems, rainbow trout, the nonanadromous form of *O. mykiss*, and steelhead are sympatric and naturally interbreed (Zimmerman and Reeves 2000). Although this would explain the lack of parent assignments of the remaining juveniles, no rainbow trout population exists in Snow Creek (Thom Johnson, Washington Department of Fish and Wildlife, 283236 Highway 101, Port Townsend, WA 98368, U.S.A., personal communication). Finally, some juveniles might have been cutthroat trout (*Oncorhynchus clarki*) or interspecific hybrids, which are nearly impossible to distinguish from steelhead at small sizes in the field without killing the fish. Indeed, using a single, powerful genetic marker (GH2D; Baker et al. 2002), four of the remaining juveniles were genetically identified as hybrids, although their actual parentage cannot be verified.

In summary, size at age may determine later life history strategies (Metcalfe and Thorpe 1992), which may in turn affect future patterns of survival and reproductive success (Ward et al. 1989). The lack of a significant relationship between either parental size or reproductive timing and the number of offspring was surprising, given the significant relationships between these parental characteristics and size of offspring that we observed and the apparent size-selective mortality in juvenile salmonids (e.g., Einum and Fleming 2000). The family-specific survival rates were probably determined by physical attributes of the breeding sites, which we could not sample, and compensatory processes occurring before our first sampling period, at the end of the first summer. Future research on salmonids should relate parental traits to the breeding site conditions and to the number, size, and migration date of smolts and their subsequent survival at sea. In addition, patterns may be very strong in a given year but not represent general selective forces and population responses; therefore, field studies need to be carried out over several years to be meaningful (also see Dickerson et al. 2002).

Acknowledgements

We thank Thom Johnson, Randy Cooper, and Cheri Scalf, Washington Department of Fish and Wildlife, for providing adult phenotypic data and for collecting all adult tissue samples and Kevin Brinck for help with statistical analyses. Additional thanks go to the long list of people who helped sample juveniles each year and to the many people who provided advice and assistance in the laboratory. The H. Mason Keeler Endowment provided financial support while this research was conducted. This material is based on work supported by the National Science Foundation under grant. No. 9903914.

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Variation in the population biology of protogynous coral reef fishes over tens of kilometres

Nick Gust

Abstract: This study describes changes in the timing of maturation and sex reversal and shifts in the sexual composition of unfished local populations of protogynous reef fishes across the continental shelf of the Great Barrier Reef. On outer shelf reef crests, both *Chlorurus sordidus* and *Scarus frenatus* matured as females and underwent protogynous sex reversal at reduced sizes and ages relative to fish from equivalent mid-shelf habitats 20 km away. Earlier maturation at smaller body sizes on the outer shelf is likely to be an adaptive response to the higher mortality rates in these habitats compared with the mid-shelf. Furthermore, reduced size and age at sex reversal on the outer shelf is consistent with the reduced growth and increased mortality regimes in these locations. The sexual composition of local populations changed markedly across the shelf for *C. sordidus* but not for *S. frenatus*. High densities of *C. sordidus* on the outer shelf were characterized by threefold higher proportions of both terminal-phase and primary males than on mid-shelf reefs. Differences between local populations separated by tens of kilometres highlight the danger of assuming homogeneous sexual compositions and life histories when managing exploited reef fishes over larger spatial scales.

Résumé : On trouvera ici une description des changements observés, à travers le plateau continental sur les récifs de la Grande Barrière, dans la phénologie de la maturation et de l'inversion sexuelle, ainsi que dans la composition sexuelle des populations locales de poissons protogynes non soumises à la pêche. Sur les crêtes des récifs externes du plateau, *Chlorurus sordidus* et *Scarus frenatus* atteignent, tous deux, la maturité comme femelles et subissent un changement de sexe protogyne à des tailles et des âges inférieurs à ceux des poissons dans des habitats semblables au milieu du plateau à 20 km de distance. La maturation précoce à une taille inférieure vers l'extérieur du plateau est sans doute une réaction adaptative aux taux de mortalité plus élevés dans ces habitats par comparaison à ceux du milieu du plateau. De plus, la taille et l'âge réduits au moment de l'inversion sexuelle sur le plateau extérieur correspondent à une croissance ralentie et un régime de mortalité accrue. La structure sexuelle des populations locales change de façon marquée chez *C. sordidus* à travers le plateau, mais non chez *S. frenatus*. Les fortes densités de *C. sordidus* sur les récifs externes du plateau se caractérisent par des proportions trois fois plus grandes de mâles en phase terminale et de mâles primaires que sur les récifs du milieu du plateau. Ces différences entre des populations locales séparées par des dizaines de kilomètres mettent en évidence le danger qu'il y a à présumer de l'existence de structures sexuelles et de cycles biologiques homogènes dans la gestion à des échelles spatiales plus grandes des poissons de récifs exploités.

[Traduit par la Rédaction]

Introduction

Marine organisms with dispersive larval propagules are predicted to benefit from plasticity in the timing of major life history events in response to variable and unpredictable physical and social environments encountered after settlement (Warner 1991; Scheiner 1993). Coral reef fishes with dispersive larvae typically become site-attached as adults in spatially heterogeneous habitats and can develop striking differences in social and mating systems between localities (Shapiro 1991). If the local density, mortality, and growth regimes experienced by particular taxa vary through space, then the life history characteristics of individuals and demography of local populations should reflect these changes over similar spatial scales.

To date, most studies of spatial variability in coral reef fish demography and population biology have concentrated on small-bodied fish such as labrids and pomacentrids (e.g., Warner and Hoffmann 1980*a*, 1980*b*; Doherty and Fowler 1994) that occupy home ranges of metres to hundreds of metres and can be studied at these small scales. Because ecologically important patterns and processes occur at differing, but explicit, scales, the spatial scale at which a system is explored will determine which patterns are detected and which are missed (Sale 1998). As principles of reef fish ecology, established largely through work on small-bodied taxa, are explored for larger and more mobile taxa, the minimum spatial

Received 8 January 2003. Accepted 30 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 25 March 2004.
J17271

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 doi: 10.1139/F03-160 © 2004 NRC Canada

scales must increase (Kritzer 2002). Studies that examine a variety of aspects of population biology are rare for large reef fish but are needed to identify which traits exhibit variation and the spatial scales on which they vary (Kritzer 2002).

Natural variation in the demography and life histories of fishes on reefs separated by tens of kilometres may confound spatially based fisheries management practices operating over larger scales. Coral reef fisheries typically target large, mobile species (Jennings and Lock 1996), and management practices often consider species to be relatively homogeneous in demography and to consist of individuals with similar life history characteristics over large spatial scales extending to hundreds of kilometres. If differences in population parameters exist over tens of kilometres, many variables such as abundance, body size, age structure, age at maturation, and sexual composition of populations used to infer the effects of fishing between locations (Russ 1991) may be unreliable indicators of impact.

This study investigates spatial variability in the reproductive biology and sexual composition of two species of unharvested scarid fishes known to differ in size across the continental shelf of the northern Great Barrier Reef (GBR) (Gust et al. 2001). Fork lengths of scarid fishes on outer shelf reef crests were 30% smaller on average than for conspecifics on mid-shelf reef crests only 20 km away. Smaller body sizes on the outer shelf were documented in eight species including *Chlorurus sordidus* and *Scarus frenatus* (Gust et al. 2001). These body size differences reflect significant changes in the shape of growth curves and reduced asymptotic sizes on the outer shelf (Gust et al. 2002). Furthermore, these species experienced higher mortality rates and reduced longevity on outer shelf reefs than on mid-shelf reefs (Gust et al. 2002). Such differences in growth and mortality could have profound life history consequences (Stearns 1992) and may alter timing in the key life history events of maturation and sex reversal for both species between shelf positions.

Life history theory enables qualitative predictions of the relative timing of maturation and sex reversal between local populations of sequentially hermaphroditic species. The key assumption in these predictions is that the timing of both events should be flexible and respond to local conditions to maximize an individual's reproductive success. Age at maturity should respond to differences in mortality schedules, which can greatly influence the reproductive fitness of individuals (Stearns 1992). Both Reznick et al. (1990) and Kozlowski (1992) suggested that reduced adult survival should promote earlier maturation and increased reproductive effort in fishes. As such, both *C. sordidus* and *S. frenatus* should mature at younger ages on outer shelf reefs than on mid-shelf reefs. Maturation in many organisms is also accompanied by a decrease in or cessation of growth (Bernado 1993), and Sadovy (1996) suggested that sexual maturity in fishes tends to coincide with growth approaching an asymptote. Since growth curves approach an asymptote at smaller sizes for both species on the outer shelf (Gust et al. 2002), maturation should occur at smaller sizes as well as younger ages for both species on the outer shelf.

Differences in growth and mortality rates between locations are also predicted to influence the timing of sex reversal in hermaphroditic fishes (Sadovy and Shapiro 1987). In protogynous reef fishes (where some females undergo sex reversal to males), environmentally mediated sex change appears to be the rule rather than the exception (Warner 1988). It is widely accepted that male reproductive success and the timing of sex reversal in hermaphroditic fish depend on the prevailing social system (e.g., Shapiro 1991), the number of females available for mating, and the number of males with whom those matings must be shared (Warner 1988). In turn, social systems and the composition of populations can be strongly influenced by local density (Warner and Hoffmann 1980*a*, 1980*b*).

The most broadly accepted hypothesis about sex change in fishes is termed the size advantage model and suggests that if the expected number of offspring produced differs between the sexes with size or age, then an individual that changes sex can take advantage of these differences and have more offspring than an individual that remains exclusively male or female (Warner 1988). Warner (1975) used simulations based on the size advantage model to show that the age of sex reversal in hermaphroditic fishes should decrease as mortality rates increase. As such, individuals of both *C. sordidus* and *S. frenatus* on outer shelf reef crests are predicted to undergo sex reversal at younger ages than conspecifics on exposed reef crests of the mid-shelf.

Accordingly, the major aim of this study was to investigate the effects of differing growth and mortality regimes on timing of maturation and sex change in local populations of two protogynous reef fishes. The study also aimed to describe spatial differences in the sexual composition of local populations of both *C. sordidus* and *S. frenatus* across the continental shelf of the northern GBR. Underwater visual censusing (UVC) was used to quantify local abundances of these fish and to estimate proportions of initial- and terminal-phase coloration. Otolith ageing combined with histological examination of gonads was used to investigate demographic patterns and shifts in the timing of maturation and sex reversal for both taxa between mid- and outer continental shelf reefs.

Materials and methods

Study species

This study examines two common and widely distributed scarids: *C. sordidus* and *S. frenatus*, since previous research indicated that they differ significantly in body sizes, growth, and mortality rates between mid- and outer continental shelf positions (Gust et al. 2001, 2002). Both taxa are readily identified in the field and the annual nature of otolith markings has been validated for both species on the northern GBR (Choat et al. 1996). Validated annual otolith increments facilitate rigorous comparison of age-specific sexual development between shelf positions. Scarids are typically protogynous hermaphrodites and males and females display different colour phases (Choat and Robertson 1975). As a result, UVC techniques can provide estimates of sexual composition in local populations. Furthermore, scarids are moderately site-attached and unlikely to move between reefs or across the continental shelf, so patterns of sexual composition and life history characteristics should reflect local conditions rather than different ontogenetic stages of dispersing adults.

Study sites

Research was conducted over 18 exposed reef crest sites on the windward (eastern) sides of three mid- and three outer shelf reefs on the northern GBR (Fig. 1). Three sites

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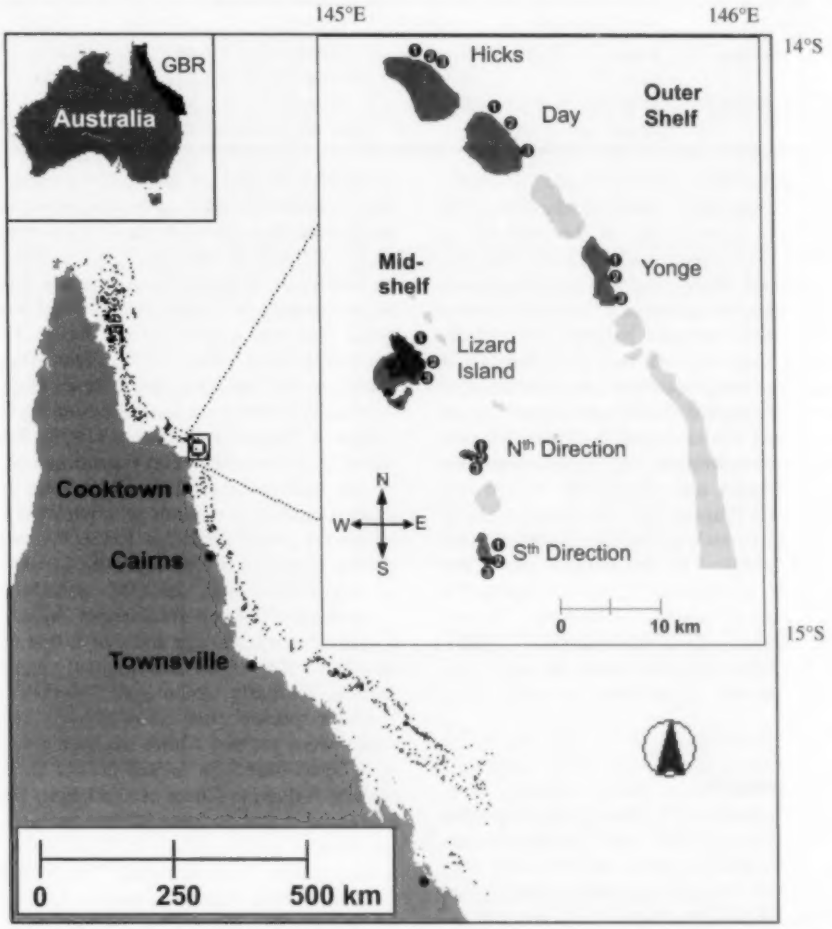
Fig. 1. The six reefs surveyed and sampled on mid- and outer continental shelf positions on the northern Great Barrier Reef (GBR), Australia. Replicate sample sites on each reef are indicated.



were surveyed on each of the mid-shelf reefs Lizard Island and North and South Direction islands and the outer shelf reefs Yonge, Hicks, and Day. Reefs and sites were chosen randomly from available locations subject to the constraints of travelling time from Lizard Island and suitable anchorages. This design ensured large sample sizes for comparison of equivalent habitat zones on the mid- and outer shelf and provides demographic information broadly representative of local populations on exposed reef crests. Because existing evidence strongly indicated that major differences in the demographic characteristics of both species exist only between shelf positions and not among replicate reefs within shelf positions (Gust et al. 2001, 2002), UVC and reproductive data were pooled at the shelf level for both species.

Underwater visual surveys

The author conducted all UVC surveys on SCUBA in 2–6 m of water at each site. Species abundance data from parrotfishes encountered on six replicate 45 m by 6 m transect swims at each site were recorded on waterproof data sheets. Individuals were identified to species and classified by colour phase along with an estimate of their fork length. Length estimates were made to the nearest 4-cm size class, and individuals were only included in the census if greater than 10 cm in total length. The choice of 10 cm as the smallest size class to be surveyed reflected a conservative approach that aimed to avoid difficulties in identifying small, typically cryptic juvenile scarids that often school together and share common colour patterns (Bellwood and Choat 1989). Each day before visual censusing, the total lengths of 20 wooden parrotfish models were estimated underwater and compared with their known lengths. This procedure aided accurate estimation of sizes, typically to within ±2 cm of true lengths, so no conversion factor was required to convert estimates to actual sizes (Gust et al. 2001). Operational sex ratios (i.e., numbers of mature female to mature males) were determined from UVC ratios of initial-phase (IP) to terminal-phase (TP) fish corrected by the proportions of IP fish that were mature females and primary males in each shelf position. These proportions were determined by histological investigation of over 300 individuals of each species.

Sampling procedures

After visual surveys were complete on each reef, hand spears were used to collect *C. sordidus* and *S. frenatus* from nine windward reef crest sites in both mid- and outer shelf

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Table 1. Sample sizes for *C. sordidus* and *S. frenatus* collected from the northern Great Barrier Reef pooled over the austral summers of 1996 and 1997.

Species	Shelf position	November	December	February	March
C. sordidus	Mid-	48	226	46	0
	Outer	44	44	141	104
S. frenatus	Mid-	46	275	59	0
	Outer	47	9	7	18

positions (Fig. 1). A total of 661 *C. sordidus* and 525 *S. frenatus* were collected between November and March in 1996 and 1997 (Table 1). Differences existed in the peak timing of collections between shelf positions; however, observations of spawning behaviour throughout this period suggests that multiple batch spawning occurred and that reproductive data are broadly comparable between habitats. To broadly characterize populations from exposed reef crest habitats in each shelf position, sites were separated by hundreds to thousands of metres on each reef. Fish were stored on ice and returned to the Lizard Island research station for processing the same day. Each individual's fork length was measured to the nearest millimetre and whole-body weight was recorded to the nearest gram. Sagittal otoliths were removed, cleaned, washed in ethanol, and stored dry before ageing. Gonads were removed, weighed to the nearest gram, and stored whole in FAACC fixative (4% formaldehyde, 5% acetic acid, 1.3% calcium chloride dihydrate) before histological investigation of reproductive status. Gonadosomatic indices (GSIs) were calculated for each individual as the gonad's percent contribution to total body weight.

Reproductive and age analysis

In protogynous species, males may develop directly from the larval stage or may develop from adult females by sex reversal. The former are called primary and the latter secondary males. Species with one development pathway, i.e., where all males arise from sex change, are monandric, whereas species with both male development pathways are labelled diandric (Sadovy and Shapiro 1987). From collections on the southern GBR, Choat and Robertson (1975) classified *C. sordidus* as a diandric species and noted that *S. frenatus* was weakly diandric with very rare primary males present in the population.

Histological techniques were used to identify immature and mature females, transitional sex changing individuals (here after referred to as transitionals), and primary and secondary males. To avoid bias, gonads were processed and staged in random order without knowledge of the collection site or the species, size, age, or colour phase of the fish. Initially, gonads from 40 individuals of both species were subsampled in anterior, mid-, and posterior locations to determine whether consistent differences in reproductive status result from the sectioning location along the length of the gonad. No evidence existed for variation in development status along the length of gonads in either species, and subsequent histological staging was based on the central section of each gonad. Gonad lobes were cut transversely into 3-mm tissue blocks, placed into cassettes, and stored in 70% ethanol.

Standard histological techniques for teleost gonads were adopted, with gonad sections being infiltrated and embedded in paraffin, sectioned at 5 µm thickness, placed onto slides, and stained with Mayers haematoxylin and Young's eosin–erythrosin. Females were classified histologically as immature (stage 1 and 2 oocytes, i.e., chromatin nucleolar and perinucleolar stages), maturing (stage 3 oocytes, i.e., cortical alveoli stage), or mature (stage 4 and 5 oocytes, i.e., vitellogenic and ripe stages) on the basis of the most advanced oocytes present (West 1990). Transitionals were classified according to Sadovy and Shapiro (1987), and primary and secondary males were classified on the basis of criteria presented in Shapiro and Rasotto (1993). Individuals were classified as males rather that transitional if there was evidence of vas deferens formation and mature spermatozoa even if ovarian regression was not yet completed and oocytes persisted within the gonad (Hastings 1981). Primary male gonads were readily identified macroscopically, as they are large and white in comparison with the pink gonads of other IP female *C. sordidus*. Percent frequencies were calculated for each sexual category, and age and size at first maturity were defined as when >50% of the histologically examined females were mature. Similarly, mean age at sex reversal was estimated for both species when >50% of the final proportion of TP males were present within the local population. Individuals were aged based on annuli counts from sectioned sagittal otoliths following Choat et al. (1996). Each otolith was read twice and removed from further analysis if there was a discrepancy of two or more years that could not be resolved by a third reader. Approximately 5% of all otoliths were eliminated following this procedure.

Data analyses

The following analyses were conducted for both species. One-way analysis of variance (ANOVA) was used to determine cross-shelf differences in mean abundance. The model tested the effects of shelf position (a fixed effect) using mean abundances of each species at the site level as replicates. Age at 50% maturation was determined in both shelf positions from frequency distributions of histological stage in each year class. Similarly, size at 50% maturation was determined from frequency distributions of histological stage in 20-mm fork length size classes. Before all ANOVA calculations, the assumption of homogeneity of variances was inspected via box plots of residuals, and $\log_{10}(X + 1)$ transformations were used to remove heterogeneity of variances as required. Ratios of IP to TP fish, operational sex ratios, and the proportions of primary males in *C. sordidus* populations were compared across the shelf by two-way contingency tables and chi square statistics using raw frequencies.

Results

Chlorurus sordidus and *S. frenatus* were collected across the continental shelf in the summer months of 1996 and

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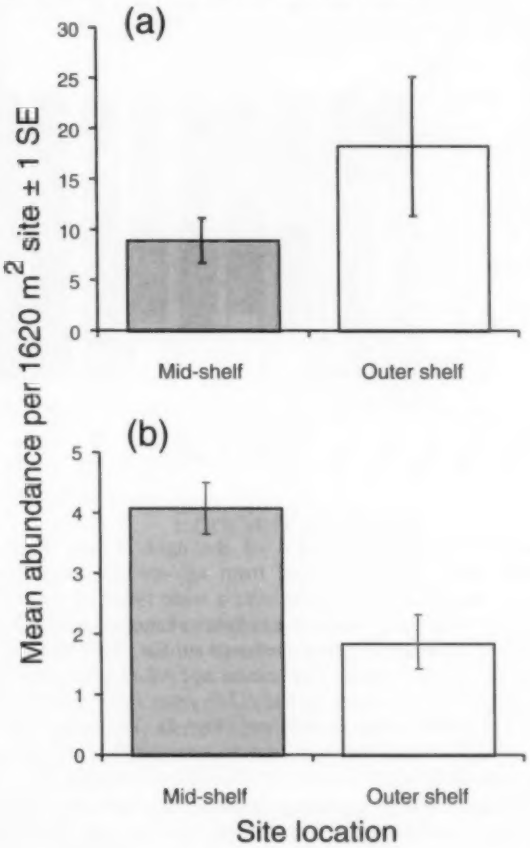
Table 2. Summary of previous research findings for *C. sordidus* and *S. frenatus* populations on mid- and outer continental shelf positions on the northern Great Barrier Reef from Gust et al. (2002).

Species	Shelf position	Growth parameter (±1 SE)	Mortality rate	Mean age (years) (± 1 SE)
C. sordidus	Mid-	K = 1.10±0.50 L_∞ = 192±4 mm	Low, M = 0.31	2.73±0.15
	Outer	K = 1.10±0.30 L_∞ = 158±4 mm	High, M = 0.49	1.85±0.10
S. frenatus	Mid-	K = 0.80±0.20 L_∞ = 255±5 mm	Low, M = 0.24	4.87±0.21
	Outer	K = 1.10±0.40 L_∞ = 196±4 mm	High, M = 0.40	2.92±0.17

Note: Growth parameters are derived from von Bertalanffy growth equations. K is the growth coefficient that describes the rate at which the asymptotic size L_∞ is approached. L_∞ is the mean asymptotic length of fish if they were to grow indefinitely. Natural mortality rate (M) is derived from the slope of a regression line plotted from the natural logarithm of the number of fish sampled in each age class.

Fig. 2. Mean abundance of (*a*) *C. sordidus* and (*b*) *S. frenatus* from exposed reef crest sites on the mid- and outer shelves.



1997, and sample sizes differed between months (Table 1). Previous research findings for these species across the shelf on the northern GBR are summarized from Gust et al. (2002) and provide information for interpreting shifts in maturation and sex change characteristics and population structures (Table 2). Differences in von Bertalanffy growth parameters, mortality regimes, and average age existed for both taxa between mid- and outer continental shelf positions. On the mid-shelf, both *C. sordidus* and *S. frenatus* achieved larger L_∞ values (mean asymptotic length of fish if they were to grow indefinitely) and asymptotic body sizes, lower rates of natural mortality, and higher average ages than on the outer shelf (Table 2).

Table 3. Comparison of mean abundances for *C. sordidus* and *S. frenatus* between sites on the mid- and outer continental shelves.

Species	Source of variation	df error	MS error	F	p
C. sordidus	Shelf position	1	395.1	4.7	0.046*
	Residual	16	84.3		
S. frenatus	Shelf position	1	22.6	12.1	0.003**
	Residual	16	1.9		

Note: *, $p < 0.05$; **, $p < 0.01$.

Distribution and abundance

UVC surveys revealed differences in the relative and absolute abundance of both species across the shelf. *Chlorurus sordidus* mean abundances at the site level were between 2- and 10-fold higher than those of *S. frenatus*, and the abundance of both species varied significantly across the shelf (Fig. 2). *Chlorurus sordidus* was more abundant on the outer shelf than on the mid-shelf (Fig. 2; Table 3), whereas *S. frenatus* was more abundant on the mid-shelf than on the outer shelf (Fig. 2; Table 3).

Maturation

Maturation in *C. sordidus* occurred at smaller sizes and younger ages on outer barrier reefs than on mid-shelf reefs. Fifty percent maturation levels were achieved once individuals reached the 161–180 mm fork length size class on the mid-shelf but occurred in the 100–120 mm size class on the outer shelf (Fig. 3). Fifty percent maturation was achieved in the 1-year age class on the mid-shelf and in the 0-year age class on the outer shelf (Fig. 4). Mean female gonadosomatic indices in the 0-year age class fish were significantly higher on the outer shelf than on the mid-shelf (ANOVA, $F_{[1,96]}$ = 10.3, p = 0.0018), which also suggests earlier sexual maturation on the outer shelf. Thus, *C. sordidus* typically matured in the 0-year age class at fork lengths above 100 mm on

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Fig. 3. Female *C. sordidus* frequency distribution of maturational stages on (*a*) the mid-shelf and (*b*) the outer shelf. Open bars, immature females; hatched bars, maturing females; solid bars, mature females. Sample sizes are indicated for each class.

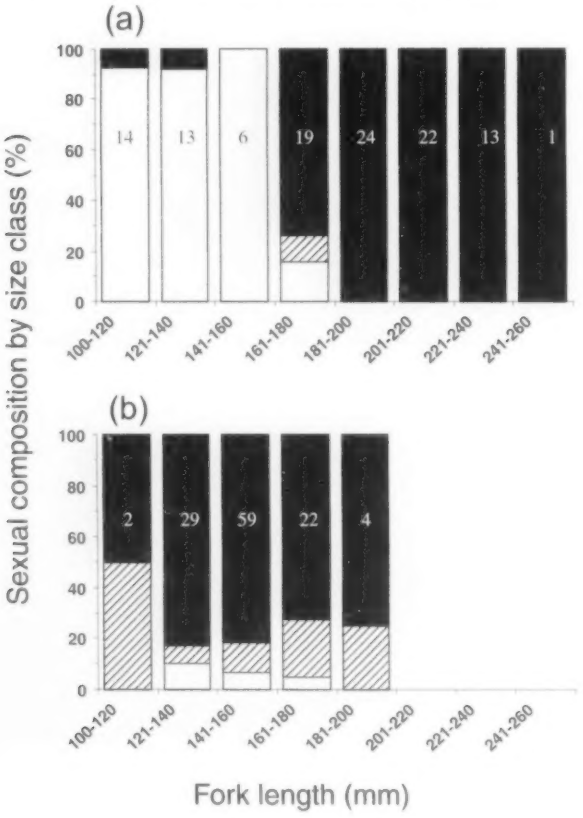
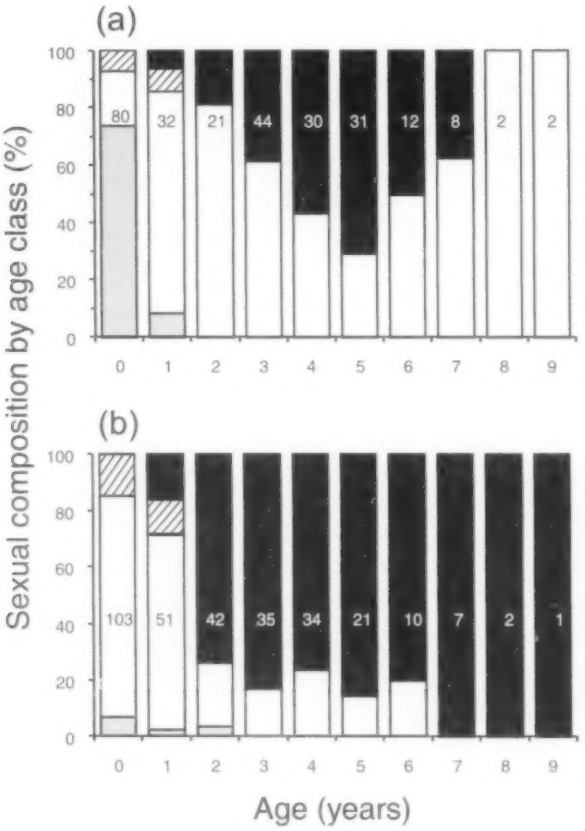


Fig. 4. *Chlorurus sordidus* age-based sexual frequencies on (*a*) the mid-shelf and (*b*) the outer shelf. Shaded bars, immature females; open bars, mature females; hatched bars, primary males; solid bars, terminal males. Sample sizes are indicated for each class.



outer shelf reefs but did not mature until reaching the 1-year age class and fork lengths above 161 mm on the mid-shelf.

Maturation in *S. frenatus* on the outer shelf also occurred at smaller sizes and younger ages than on the mid-shelf. Fifty percent maturation occurred in the 221–240 mm fork length size class on the mid-shelf and in the 181–200 mm size class on the outer shelf (Fig. 5). Fifty percent maturation was achieved in the 2-year age class on the mid-shelf and in the 1-year age class on the outer shelf (Fig. 6). Thus, *S. frenatus* maturation typically occurred above 181 mm fork length as 1-year-olds on outer shelf reefs but was delayed until individuals reached 2 years of age and fork lengths exceeded 221 mm on the mid-shelf.

Protogynous sex change

Protogynous sex reversal was confirmed from the presence of sex-changing individuals in both species. Individuals captured in transitional colour phases were functional males in both species, indicating that functional sex change precedes colour changes in these scarids. The number of individuals detected with transitional gonads was low (<1% of individuals), especially for *S. frenatus*, such that statistical comparison of their characteristics was precluded. The low numbers of transitional individuals sampled for both species precluded precise definition of the ages at sex reversal, which were inferred instead from age-specific sexual patterns. Sex reversal occurred over a wide range of sizes and ages for both taxa, although estimates of mean age at sex reversal in both species were reduced on the outer shelf relative to the mid-shelf. The mean age of sex reversal for *C. sordidus* was approximately 2.5 years on the mid-shelf and 1.5 years on the outer shelf (Fig. 4). The mean age of sex reversal for *S. frenatus* was approximately 3.5 years on the mid-shelf and 2.5 years on the outer shelf (Fig. 6).

TP males of both species on the outer shelf were significantly smaller and younger than conspecifics on the mid-shelf (Fig. 7; Table 4). On the outer shelf, *C. sordidus* TP males were on average 47 mm shorter in fork length than those on the mid-shelf (Fig. 7*a*; Table 4). On the outer shelf, *C. sordidus* TP males were on average 0.6 year younger than those on the mid-shelf (Fig. 7*b*; Table 4). The mean fork length of *S. frenatus* TP males on the outer shelf was 77 mm smaller than on the mid-shelf (Fig. 7*c*; Table 4). The mean age of *S. frenatus* TP males on the outer shelf was significantly younger, by 2.0 years, than on the mid-shelf (Fig. 7*d*; Table 4).

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Fig. 5. Female *S. frenatus* frequency distribution of maturational stages on (*a*) the mid-shelf and (*b*) the outer shelf. Open bars, immature females; hatched bars, maturing females; solid bars, mature females. Sample sizes are indicated for each class.

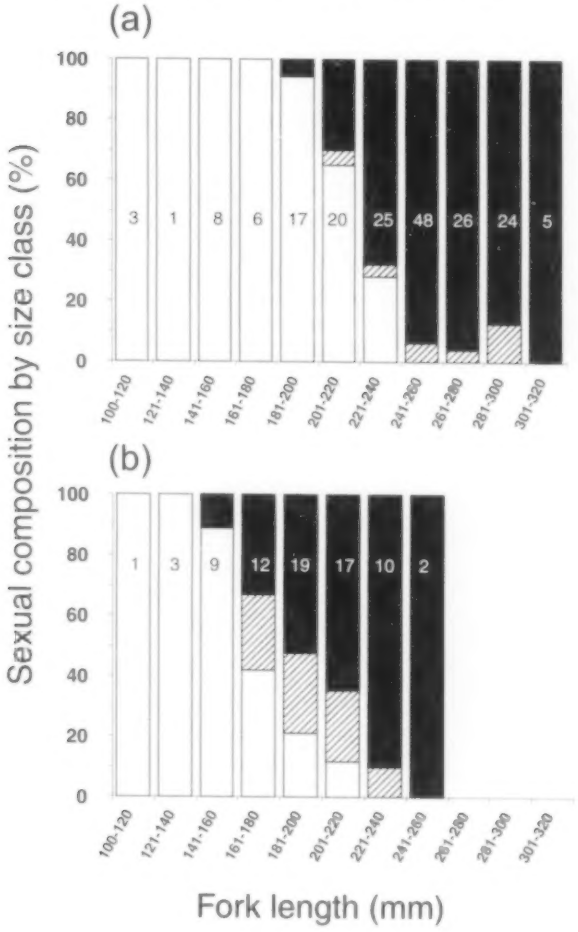
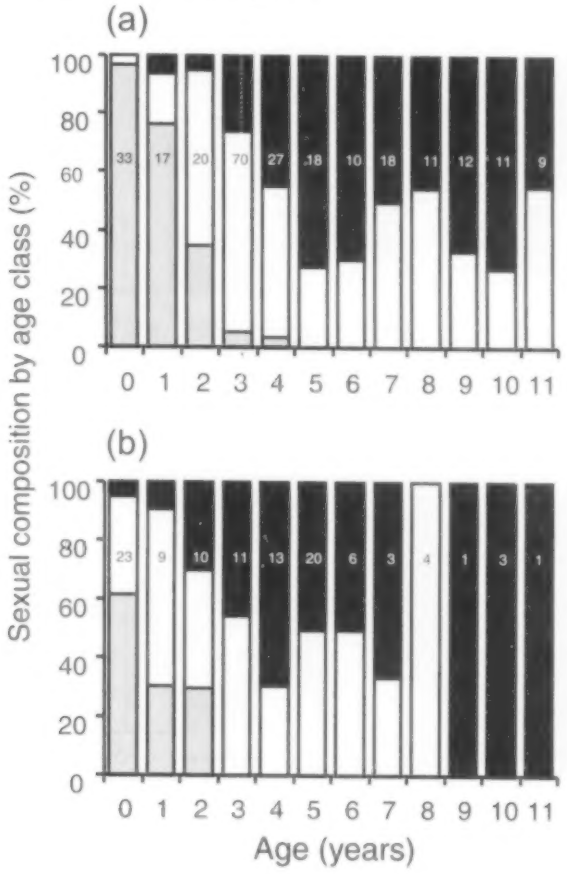


Fig. 6. *Scarus frenatus* age-based sexual frequencies on (*a*) the mid-shelf and (*b*) the outer shelf. Solid bars, terminal-phase males; open bars, mature females; shaded bars, immature females. Sample sizes are indicated for each age class.



Population structures and sex ratios

Age-based population structures differed markedly between shelf positions for *C. sordidus* (Fig. 4). On the mid-shelf, females persisted through all age classes, and the proportion of TP males increased to age 5 and then declined (Fig. 4*a*). On the outer shelf, no females persisted beyond age 6 and TP males represented more than 70% of each age class older than 1 (Fig. 4*b*). Age-based population structures differed slightly between shelf positions for *S. frenatus*, although small sample sizes in the oldest age classes on the outer shelf make comparisons difficult (Fig. 6). Females persist to age 11 on the mid-shelf but only to age 8 on the outer shelf, although approximately 50% of fish from ages 8 to 11 are females in each shelf position (Fig. 6).

Plots of GSI versus fork length for different sexual categories revealed cross-shelf differences in both species. For *C. sordidus*, the proportion of primary males increased significantly ($\chi^2 = 47.7$, df = 1, $p < 0.001$) from the mid-shelf to the outer shelf (Fig. 8). Histology confirmed that 4.0% of IP fish on the mid-shelf were primary males as opposed to 12.9% on the outer shelf. Mid-shelf primary males displayed low GSI values (mean 0.1) that were equivalent to values for secondary males (Fig. 8*a*). However, outer shelf primary males displayed 20 times higher GSI values (mean 2.0) that were similar to values for mature females (Fig. 8*b*). Plots of GSI versus fork length for *S. frenatus* indicated that 10% of TP males on the mid-shelf possessed large gonads (GSI > 0.5) that were of similar proportions to mature female gonads (Fig. 9*a*). However, on the outer shelf, all TP males had small GSI values, with an average of 0.1 (Fig. 9*b*).

UVC surveys indicated marked differences in *C. sordidus* size distributions between shelf positions, where the largest size classes for both colour phases on the mid-shelf were missing for outer shelf positions (Figs. 10*a* and 10*c*). There were significant changes in IP to TP ratios between mid- and outer shelf populations ($\chi^2 = 60.6$, df = 1, $p < 0.001$), with TP fish being three times more common on the outer shelf (Figs. 10*a* and 10*c*). Operational sex ratios for *C. sordidus* on the mid-shelf were significantly more female biased than

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Fig. 3. Female *C. sordidus* frequency distribution of maturational stages on (*a*) the mid-shelf and (*b*) the outer shelf. Open bars, immature females; hatched bars, maturing females; solid bars, mature females. Sample sizes are indicated for each class.

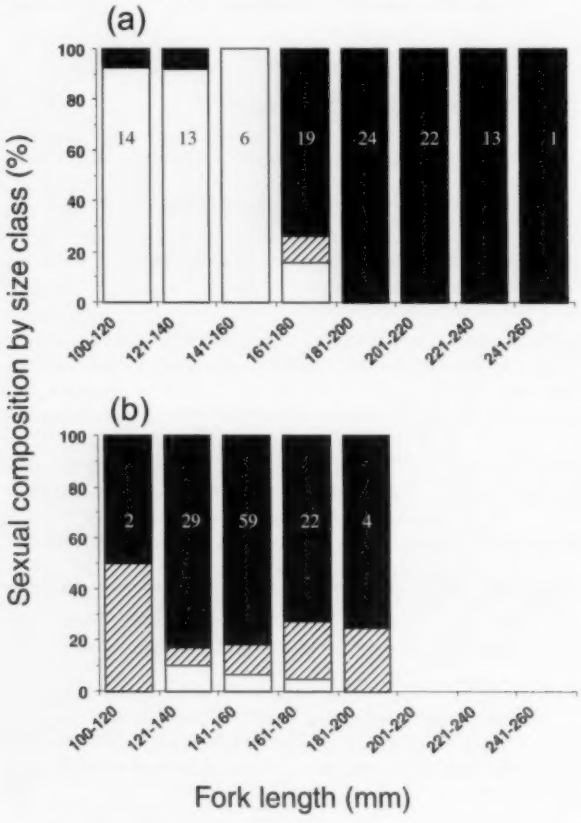
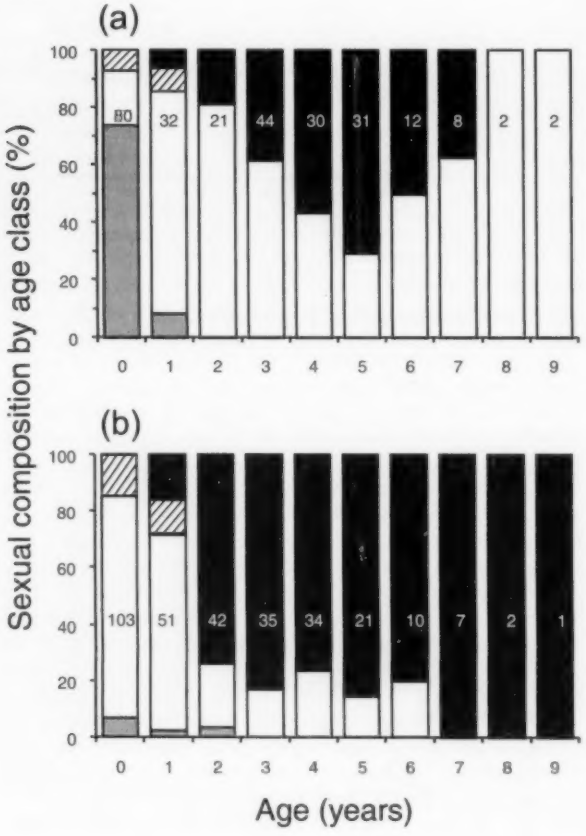


Fig. 4. *Chlorurus sordidus* age-based sexual frequencies on (*a*) the mid-shelf and (*b*) the outer shelf. Shaded bars, immature females; open bars, mature females; hatched bars, primary males; solid bars, terminal males. Sample sizes are indicated for each class.



outer shelf reefs but did not mature until reaching the 1-year age class and fork lengths above 161 mm on the mid-shelf.

Maturation in *S. frenatus* on the outer shelf also occurred at smaller sizes and younger ages than on the mid-shelf. Fifty percent maturation occurred in the 221–240 mm fork length size class on the mid-shelf and in the 181–200 mm size class on the outer shelf (Fig. 5). Fifty percent maturation was achieved in the 2-year age class on the mid-shelf and in the 1-year age class on the outer shelf (Fig. 6). Thus, *S. frenatus* maturation typically occurred above 181 mm fork length as 1-year-olds on outer shelf reefs but was delayed until individuals reached 2 years of age and fork lengths exceeded 221 mm on the mid-shelf.

Protogynous sex change

Protogynous sex reversal was confirmed from the presence of sex-changing individuals in both species. Individuals captured in transitional colour phases were functional males in both species, indicating that functional sex change precedes colour changes in these scarids. The number of individuals detected with transitional gonads was low (<1% of individuals), especially for *S. frenatus*, such that statistical comparison of their characteristics was precluded. The low numbers of transitional individuals sampled for both species precluded precise definition of the ages at sex reversal, which were inferred instead from age-specific sexual patterns. Sex reversal occurred over a wide range of sizes and ages for both taxa, although estimates of mean age at sex reversal in both species were reduced on the outer shelf relative to the mid-shelf. The mean age of sex reversal for *C. sordidus* was approximately 2.5 years on the mid-shelf and 1.5 years on the outer shelf (Fig. 4). The mean age of sex reversal for *S. frenatus* was approximately 3.5 years on the mid-shelf and 2.5 years on the outer shelf (Fig. 6).

TP males of both species on the outer shelf were significantly smaller and younger than conspecifics on the mid-shelf (Fig. 7; Table 4). On the outer shelf, *C. sordidus* TP males were on average 47 mm shorter in fork length than those on the mid-shelf (Fig. 7*a*; Table 4). On the outer shelf, *C. sordidus* TP males were on average 0.6 year younger than those on the mid-shelf (Fig. 7*b*; Table 4). The mean fork length of *S. frenatus* TP males on the outer shelf was 77 mm smaller than on the mid-shelf (Fig. 7*c*; Table 4). The mean age of *S. frenatus* TP males on the outer shelf was significantly younger, by 2.0 years, than on the mid-shelf (Fig. 7*d*; Table 4).

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Fig. 5. Female *S. frenatus* frequency distribution of maturational stages on (*a*) the mid-shelf and (*b*) the outer shelf. Open bars, immature females; hatched bars, maturing females; solid bars, mature females. Sample sizes are indicated for each class.

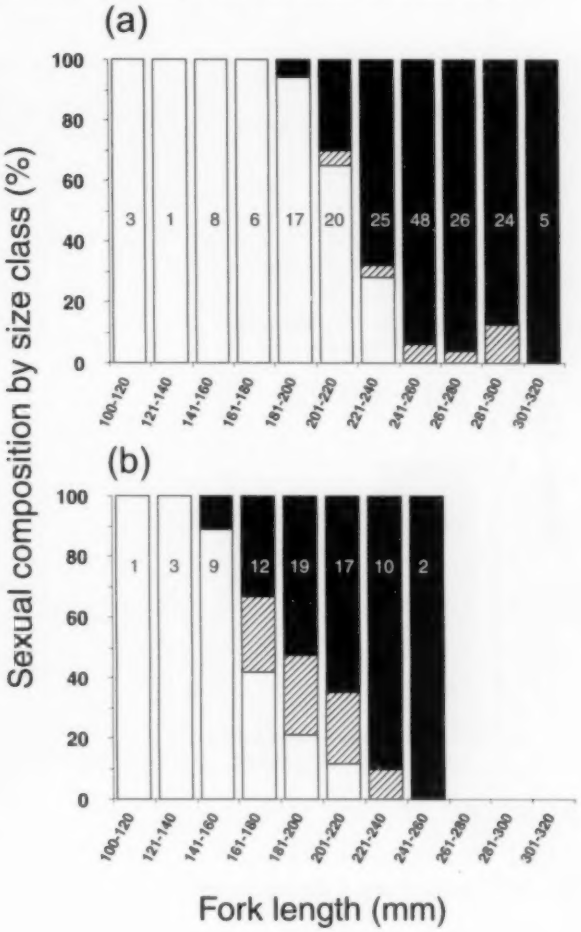
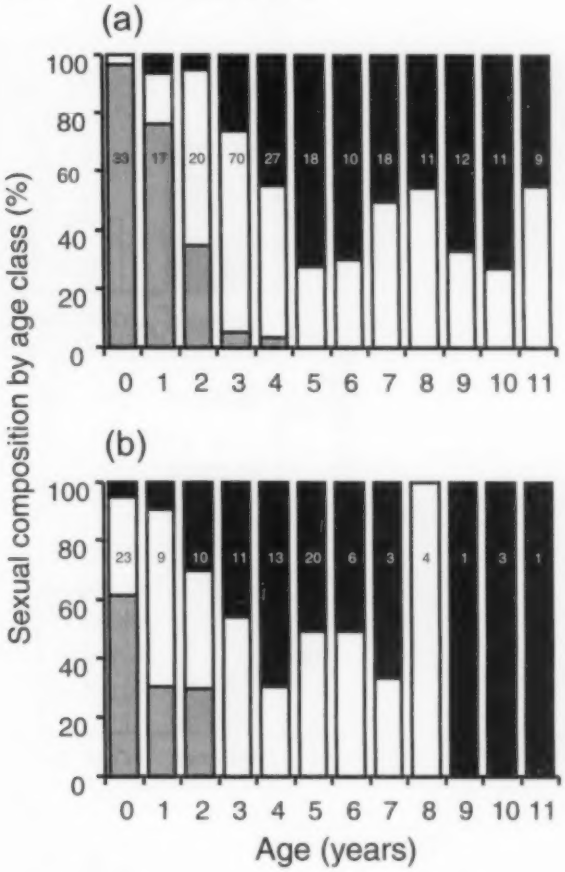


Fig. 6. *Scarus frenatus* age-based sexual frequencies on (*a*) the mid-shelf and (*b*) the outer shelf. Solid bars, terminal-phase males; open bars, mature females; shaded bars, immature females. Sample sizes are indicated for each age class.



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UVC surveys indicated marked differences in *C. sordidus* size distributions between shelf positions, where the largest size classes for both colour phases on the mid-shelf were missing for outer shelf positions (Figs. 10*a* and 10*c*). There were significant changes in IP to TP ratios between mid- and outer shelf populations ($\chi^2 = 60.6$, df = 1, $p < 0.001$), with TP fish being three times more common on the outer shelf (Figs. 10*a* and 10*c*). Operational sex ratios for *C. sordidus* on the mid-shelf were significantly more female biased than

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Fig. 7. Mean terminal-phase male size (fork length) for (*a*) *C. sordidus* and (*c*) *S. frenatus* between shelf positions. Mean terminal-phase male age (years ± 1 SE) for (*b*) *C. sordidus* and (*d*) *S. frenatus* between shelf positions.

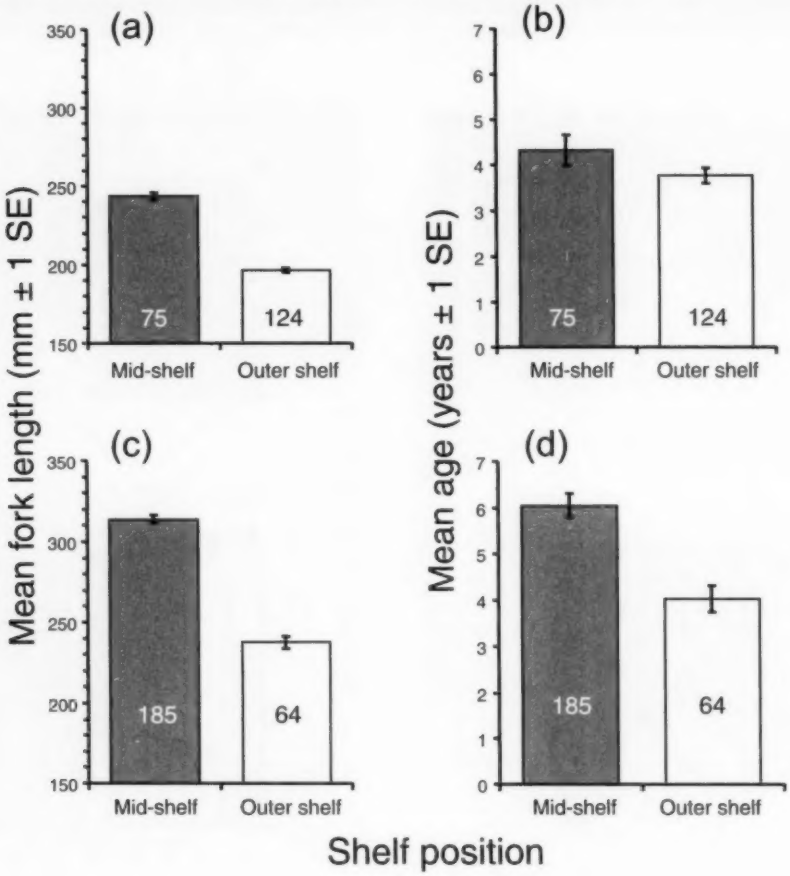

Table 4. Comparison of terminal-phase male body sizes and ages for *C. sordidus* and *S. frenatus* between mid- and outer continental shelf positions.

Species	Dependent variable	Source of variation	df	MS	*F*	*p*
C. sordidus	Size (fork length)	Shelf position	1	102 476	282.1	<0.0001***
		Residual	199	363.30		
	Age (years)	Shelf position	1	13.10	5.4	0.0217*
		Residual	199	2.40		
S. frenatus	Size (fork length)	Shelf position	1	261 321	285.1	<0.0001***
		Residual	249	916.40		
	Age (years)	Shelf position	1	222.1	22.0	<0.0001***
		Residual	249	10.10		

Note: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.0001$.

on the outer shelf ($\chi^2 = 8.39$, df = 1, $p = 0.0037$). Operational sex ratios changed by a factor of 3 from the mid-shelf (4.75:1) to the outer shelf (1.48:1).

UVC surveys indicated marked differences in *S. frenatus* size distributions between shelf positions, where the largest three size-classes on the mid-shelf were missing on the outer shelf (Figs. 10*b* and 10*d*). On the mid-shelf, IP to TP ratios (2.12:1) were 32% more female biased than on the outer shelf (1.60:1), but chi square tests indicated no significant differences across the shelf ($\chi^2 = 1.43$, df = 1, $p = 0.231$). Since no primary-phase males were identified among the 558 *S. frenatus* sampled, the species appears monandric on the northern GBR. Operational sex ratios on the mid-shelf (1.49:1) were 40% more female biased than the outer shelf (1.07:1), although chi square tests indicated no significant difference across the shelf ($\chi^2 = 0.29$, df = 1, $p = 0.591$).

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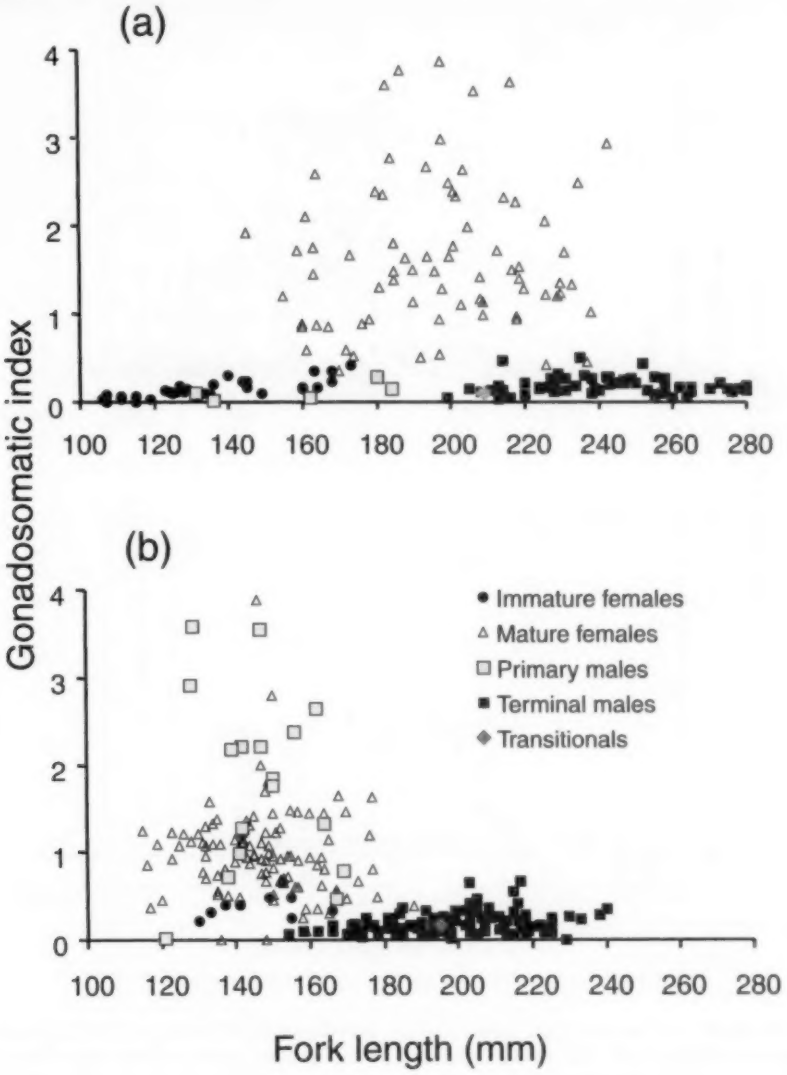
Fig. 8. *Chlorurus sordidus* gonadosomatic indices versus fork lengths on (*a*) the mid-shelf and (*b*) the outer shelf. Sexual categories were identified by histology.



Discussion

This study revealed considerable differences in the size and age at maturity and sex change in the protogynous reef fishes *C. sordidus* and *S. frenatus* across a distance of only 20 km. Both species displayed changes in size structure across this spatial scale, and *C. sordidus* demography also changed markedly, with operational sex ratios altering by a factor of 3 between mid- and outer shelf positions. Since these species are not harvested on the GBR and are not subject to any known direct anthropogenic disturbances, observed changes in the timing of major life history events and demography over tens of kilometres are likely to reflect natural variability and responses to local environmental and social conditions. *Chlorurus sordidus* mean abundance per site doubled from the mid- to the outer shelf, whereas *S. frenatus* mean abundance halved. Despite this opposite pattern in relative abundance between locations, both species matured and changed sex at reduced mean sizes and ages on the outer shelf. This suggests that conspecific density alone is not responsible for cross-shelf changes in the timing of maturation and sex reversal in both species. Rather, consistent differences in growth and mortality regimes for both species between shelf positions (Gust et al. 2002) are implicated.

Large changes in population biology over tens of kilometres may compromise fisheries management efforts over larger spatial scales. Research on predators commonly targeted in coral reef fisheries typically reports population parameters averaged across many locations or at best makes spatial comparisons on very broad scales (hundreds of kilometres or more; Newman et al. 1996). This study indicates that generalized population parameters produced over large-scale studies

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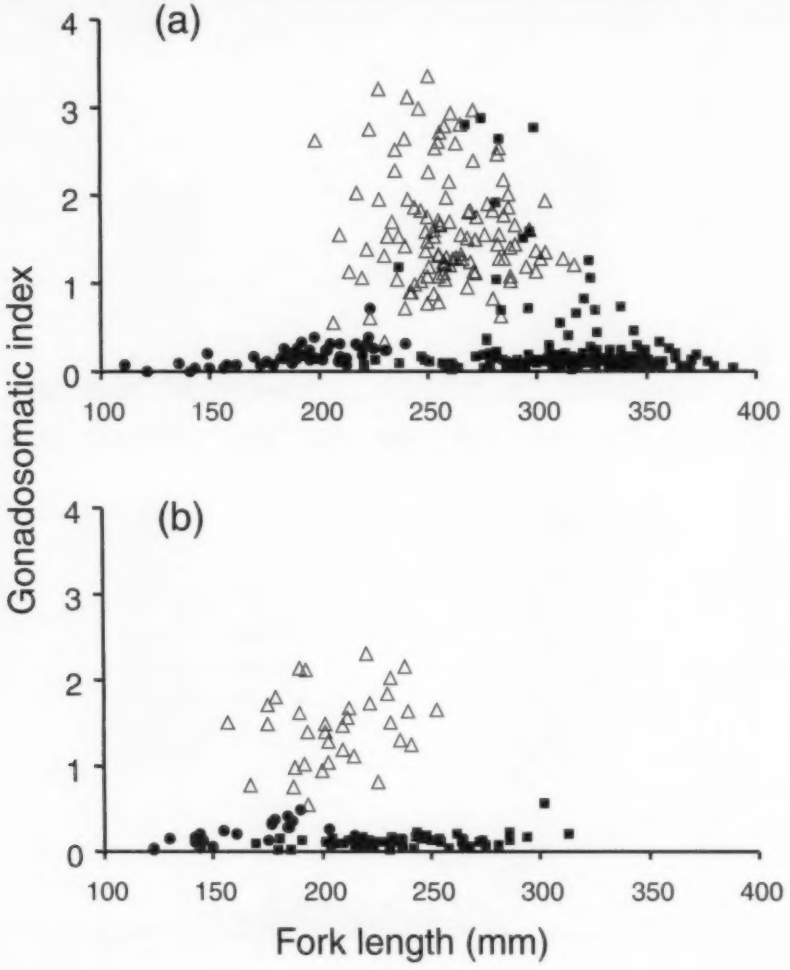
Fig. 9. *Scarus frenatus* gonadosomatic indices versus fork lengths on (*a*) the mid-shelf and (*b*) the outer shelf. Sexual categories were identified by histology. Circles, immature females; triangles, mature females; squares, terminal-phase males.



may poorly represent fishery resources, since population parameters can change markedly over tens of kilometres. Without knowledge of the spatial scales at which population parameters differ and the magnitude of this natural variation, changes between locations in population size or age structures, sex ratios, or the size and age at which individuals mature and change sex may all be unreliable indicators of anthropogenic impacts such as fishing.

Maturation

Age at maturity is one of the most important traits in the life history of an organism (Belk 1998) and has a strong effect on lifetime reproductive success and the intrinsic rate of population growth, two common measures of fitness (Reznick 1990). Although flexibility in the timing of maturation within species has previously been widely documented in fishes (Stearns 1992; Berrigan and Koella 1994), Bernado (1993) provided some rare accounts of invariant age or size at maturation within species. For instance, Jones and Thompson (1980) concluded that maturation and sex reversal in the temperate protogynous reef fish *Pseudolabrus celidotus* were more closely related to size than to age and found that maturation only occurred once a threshold body size was exceeded.

This study described flexibility in both the size and age at maturation in both *C. sordidus* and *S. frenatus*. Plasticity in the timing of maturation is generally considered to be a response to prevailing conditions, and empirical studies in teleosts using otolith ageing techniques have commonly shown a significant correlation between the age at first reproduction and both mortality and growth rates in local populations (Roff 1984). Roff (1984) proposed that the timing of maturation represented a trade-off between the demands of reproduction, growth, and survival in response to local conditions. A number of theoretical ecologists subsequently developed the concept of "optimal" ages or sizes at which maturation should occur to maximize an individual's fitness and reproductive output (Stearns and Koella 1986; Kozlowski 1992; Stearns 1992). The majority of their modelling approaches are sensitive to

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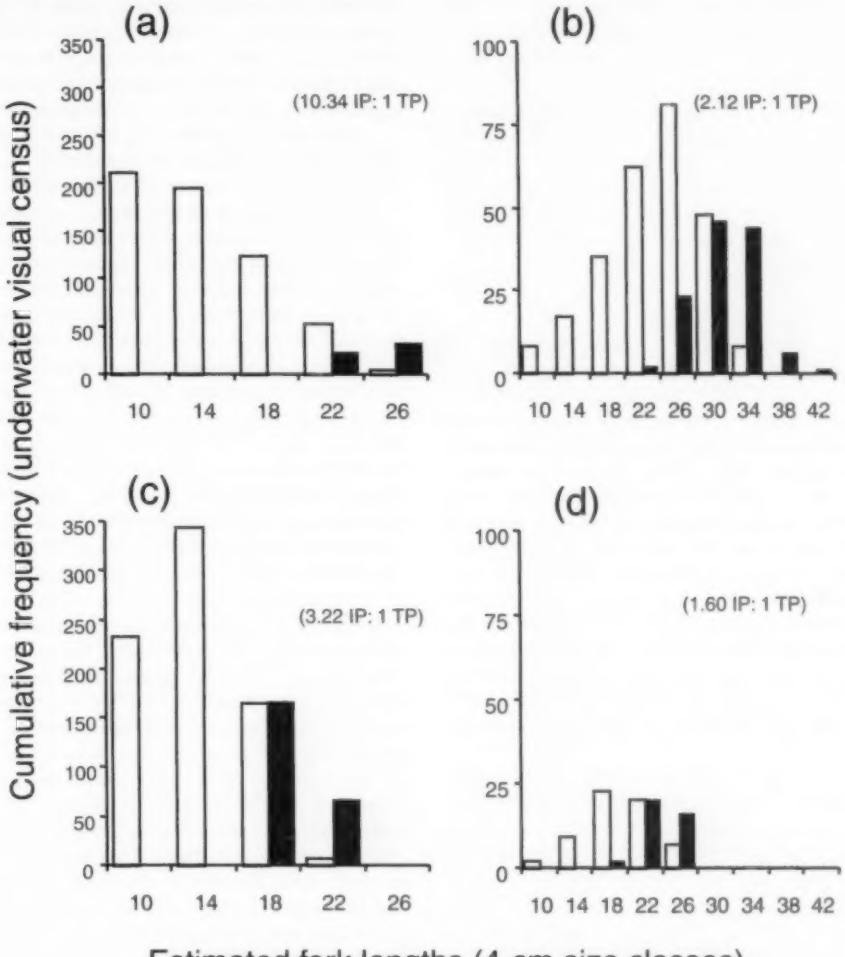
Fig. 10. Size frequency distributions estimated from underwater visual censuses across nine sites in each shelf position: (*a*) *C. sordidus*, mid-shelf, (*c*) *C. sordidus*, outer shelf, (*b*) *S. frenatus*, mid-shelf, and (*d*) *S. frenatus*, outer shelf. Open bars, initial phase (IP); solid bars, terminal phase (TP). Ratios of IP to TP fish are indicated.



varying growth and mortality regimes and attempt to predict when animals should mature to obtain the optimal balance between costs and benefits of early and late maturation.

Theoretical models typically predict that maturation should occur earlier as adult mortality rates increase or as growth increases (e.g., Roff 1984; Stearns and Koella 1986). The findings of the present study are consistent with the first but not the second prediction. Both scarid taxa were found to become sexually mature at smaller sizes and younger ages on the outer shelf where prevailing mortality rates are higher and growth is reduced in comparison with the mid-shelf (Gust et al. 2002). Thus, although the most common pattern for variation in age and size at maturity involves animals maturing later at a smaller size when growth is reduced (Stearns and Koella 1986), the reduced size and age at maturity for both species on the outer shelf is more likely to represent a response to higher natural mortality rates on the outer shelf than prevailing growth differences across the shelf. The simplest way to improve survival to maturity is to mature earlier (Bell 1980), and it appears that on outer shelf reef crests, both species respond in this way. A similar pattern of reduced growth and earlier maturation in reef fish experiencing high mortality rates has been reported by Cowen (1990) and was suggested to reflect a reallocation of energy towards earlier or more intensive reproduction at the expense of somatic growth. Sadovy (1996) suggested that sexual maturity in fishes tends to coincide with growth approaching an asymptote. Thus, reduced asymptotic sizes for both species on the outer shelf may reflect the effects of earlier maturation and allocation of energy towards reproductive development at the expense of somatic growth.

Genetic mechanisms for maturation shifts in response to higher mortality regimes and the presence of predators have been noted in teleosts. For instance, Reznick et al. (1990) experimentally demonstrated that changes in the relative mortality of different age and size classes over several generations can result in selection of fish with genetically based differences in age and size at maturity. Genetic explanations

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appear unlikely in this case, however, since both study species possess dispersive larval propagules, which are assumed to be freely exchanged between reefs in mid- and outer shelf positions. Analysis of mitochondrial DNA from *C. sordidus* and *S. frenatus* sampled during this study indicated high rates of gene flow for both species within and among shelf positions and provided no evidence of barriers to gene flow across the continental shelf (Dudgeon et al. 2000). Changes in the timing of maturation across the shelf could also reflect differences in water temperature and its effect of modifying metabolism (Jobling 1981). However, this seems unlikely in the present study, since the water body spanning mid- and outer shelf positions on the northern GBR is well mixed and has a similar temperature (Wolanski 1986).

Protogynous sex change

On the outer shelf, reduced size and age at sex reversal in both *C. sordidus* and *S. frenatus* is consistent with predictions of the size advantage model and reduced growth regimes for both species. Simulations based on the size advantage model by Warner (1975) predicted delayed sex change (and since size is loosely correlated with age, a larger size at sex change) where the rate of female increase in fecundity with age is improved. Since female fecundity in fishes is typically a function of body size, larger size achieved at a given age suggests a more rapid increase in fecundity. Since body size asymptotes at smaller sizes for both species on the outer shelf (Gust et al. 2002), female reproductive potential may be constrained in these habitats and male reproductive success may increase more rapidly with age than on the mid-shelf. As such, protogynous sex change at younger ages and smaller sizes is both predicted and observed in both species on the outer shelf.

The change in mean age at sex reversal in both species between shelf positions is also consistent with predictions of the size advantage model regarding the effects of prevailing mortality regimes. On the outer shelf, both scarids are subject to higher mortality rates than on the mid-shelf (Gust et al. 2002). Higher mortality and reduced survivorship should reduce the size and age at sex reversal in hermaphroditic species (Warner 1975; Cowen 1990). Thus, it is difficult to determine whether changes in growth or mortality regimes across the shelf have independent or additive effects on the timing of sex change in these species, since cross-shelf differences in both processes are consistent with the observed pattern. Both Jones and Thompson (1980) and Cowen (1990) have reported similar confounding of the effects of concurrent changes in mortality and growth between locations on the timing of sex reversal in protogynous fishes, such that the relative importance of each factor could not be determined.

Population structures and social systems

Studies of social and mating systems in teleost fishes have been biased towards small, easily observed and manipulated reef fishes (e.g., Cole and Robertson 1988; Warner 1988; Cole and Shapiro 1992). Detailed descriptions of these systems in many mobile, larger bodied fishes such as *C. sordidus* and *S. frenatus* are not currently available, which limits interpretation of observed changes in population structure between locations. However, we know from collections on the southern GBR that *C. sordidus* is diandric, whereas *S. frenatus* was described as weakly diandric (Choat and Robertson 1975). On the northern GBR, the present study confirmed diandric male development in *C. sordidus* but found that *S. frenatus* was monandric with no primary males in this section of its geographic range. Preliminary observations on the northern GBR suggest that *C. sordidus* displays loose groupings of IP fish in feeding schools attended by TP males that often interact aggressively, presumably in competition over females or spawning site resources. In contrast, *S. frenatus* maintains small, well-defined harems consisting of a single TP male and one to four IP females (N. Gust, personal observation).

Marked changes in population structure of *C. sordidus* between mid- and outer shelf positions suggest shifts in social and mating systems, which may represent responses to local population density. *Chlorurus sordidus* mean abundance doubled from nine individuals to 18 individuals per 1620-m^2 site between mid- and outer shelf positions. High-density local populations on the outer shelf were characterized by threefold higher proportions of both TP and primary males than on the mid-shelf, and operational sex ratios differed across the shelf from 4.7:1 to 1.5:1 (females to males). Although threefold shifts in sex ratio over 20 km appear large, sex ratios can be highly variable over even moderate spatial scales in protogynous reef fish and similar shifts have previously been documented between reefs in the goby *Corphopterous glaucofraenum* (Cole and Shapiro 1992) and the scarid *Sparisoma viride* (van Rooij et al. 1996).

In *C. sordidus*, increased proportions of primary males on the outer shelf and their large GSI values suggest that they may be involved in group spawning mating strategies in this location. Cole and Shapiro (1992) suggested that primary males might arise from an immature ovariform stage by social regulation, may be genetically determined, may be triggered by some aspect of the physical environment, or may arise from a combination of these factors. Previous studies have implicated local population density as an important factor influencing the frequency (and presumably success) of the primary male strategy in reef fishes. For instance, Warner and Hoffman (1980*a*, 1980*b*) also reported higher proportions of primary males in high-density local populations of diandric reef fish and found that this pattern arose from differences in the economic defendability of resources by larger TP males. They showed that although TP males can prevent primary males from obtaining spawning success in low-density populations, this ability diminished as population density increased. Population density has regularly been implicated in changes in the social and mating systems of coral reef fishes between localities (Shapiro 1991). This author emphasized the importance of spatially patchy recruitment in altering local population densities and influencing the development of both social systems and local population structures. Higher recruitment of *C. sordidus* to outer shelf reef crests than to equivalent mid-shelf habitats could explain higher population densities despite higher rates of natural mortality and may provide suitable reproductive opportunities for high proportions of primary males to persist in local populations.

Scarus frenatus displayed a similar age-based demographic structure in both mid- and outer shelf positions. Interestingly, some small TP *S. frenatus* on the mid-shelf displayed high GSI values equivalent to those of mature females, which suggests that they may be participating in group spawns or

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other sperm-competitive forms of mating in this location where mean densities are twice as high as on the outer shelf. Alternatively, large GSI values for these small males may indicate that they are recently sex-changed individuals where functional sex reversal is complete but gonads have not yet regressed in size. Direct observational studies to determine the prevailing social and mating systems for both species are required to interpret the differences in population structure described in this study over scales of tens of kilometres.

In conclusion, this study has revealed considerable differences in the timing of maturation and sex reversal in local populations of two unharvested protogynous reef fishes separated by only 20 km. The sexual composition and operational sex ratios for one of these species also differed markedly over this spatial scale. If equivalent levels of variability exist over such fine spatial scales for commonly harvested protogynous reef fishes such as serranids, extensive sampling will be required to assess the impacts of fishing and separate anthropogenic impacts from natural spatial variability.

Acknowledgments

Thanks are extended to the staff of the Lizard Island research station and Stuart Watson, Mark Thomas, David Kjar, David Brown, and especially Anne Trevena for invaluable assistance during the course of this study. Howard Choat, Mark McCormick, and Philip Munday made valuable comments on earlier drafts of this manuscript. This study was supported by a Lizard Island doctoral fellowship from the Australian Museum and a Queens Trust award to Nick Gust. Research was carried out under James Cook University ethics permit A468 and GBRMPA permit G96/481.

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Long-term changes in Baltic herring (*Clupea harengus membras*) growth in the Gulf of Finland

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Abstract: We used the longest available weight-at-age (WAA) time series (from 1950 to 1999) for Baltic herring (*Clupea harengus membras* L.) in the Gulf of Finland to investigate which environmental factors affect Baltic herring growth. The relationships among WAAs, annual weight increments, and growth rates for different herring year classes, water salinity, temperature, zooplankton abundance, and biomass, as well as stock sizes of herring, sprat, and cod, were evaluated. Our results showed that in the Gulf of Finland, herring weight and growth rate correlated positively with salinity, and WAA correlated positively with the abundance of the marine zooplankton species *Pseudocalanus minutus elongatus*. A density-dependent mechanism was not likely to explain the changes in herring WAA in the Gulf of Finland, because no significant correlation between herring WAAs and herring abundance could be found. Instead, the zooplankton community structure changed during the research period, which supports the theory of bottom-up controlling mechanism. A strong negative correlation between herring weight and sprat biomass may indicate competition for food between these species.

Résumé : L'utilisation de la plus longue série chronologique disponible (de 1950 à 1999) de données de masses en fonction de l'âge (WAA) des harengs de la Baltique (*Clupea harengus membras* L.) du golfe de la Finlande nous a servi à rechercher les facteurs du milieu qui affectent la croissance des harengs de la Baltique. Nous avons évalué les relations, d'une part, entre les WAA, les accroissements annuels de masse et les taux de croissance des différentes classes d'âge de harengs et, d'autre part, la salinité de l'eau, la température, l'abondance et la biomasse du zooplancton, de même que l'importance des stocks de harengs, de sprats et de morues. Chez les harengs du golfe de Finlande, il y a une corrélation positive entre la masse et le taux de croissance, d'une part, et la salinité, d'autre part, ainsi qu'entre WAA et l'abondance de l'espèce zooplanctonique marine *Pseudocalanus minutus elongatus*. Il est peu probable que le mécanisme explicatif des changements des WAA chez les harengs du golfe de Finlande soit dépendant de la densité puisqu'il ne semble pas exister de corrélation significative entre les WAA des harengs et leur abondance. Par ailleurs, la structure de la communauté zooplanctonique a changé durant la période d'étude, ce qui corrobore l'hypothèse de l'existence d'un mécanisme de contrôle ascendant. La forte corrélation négative entre la masse des harengs et la biomasse des sprats indique peut-être qu'il y a compétition pour la nourriture entre ces deux espèces.

[Traduit par la Rédaction]

Introduction

Herring has been the most successful marine fish species that immigrated into the Baltic Sea because of its high ability for adaptation. Local herring populations in various areas of the Baltic Sea are distinguished by characteristics such as feeding habits (e.g., Ojaveer and Lehtonen 2001). Feeding of Baltic herring also varies with season and age. However, despite the large temporal and spatial variations in feeding, all Baltic herring are mainly planktivores, preferring large-sized prey such as copepods (Sandström 1980; Flinkman et al. 1992; Lankov and Kukk 2002). Feeding conditions appears to affect the growth of herring; herring living on planktonic food during their whole life have stunted growth, whereas animals that have shifted to fish grow extremely well (e.g., Hessle 1937).

In the Baltic Sea, changes in herring (*Clupea harengus membras* L.) growth have been observed as long as the growth has been recorded (e.g., Strzyzewska and Popiel 1974; Ojaveer 1988). However, during the last few decades, herring growth has fluctuated remarkably. Herring weight-at-age (WAA) started to increase in the 1970s but subsequently (in 1985–1992) growth slowed and WAA declined almost by 50% in most age groups in various areas of the Baltic Sea (Anonymous 1994). Both top-down and bottom-up mechanisms and their combinations have been suggested to control herring growth and to have potentially caused this herring growth anomaly (Flinkman et al. 1998; Cardinale and Arrhenius 2000). The top-down hypothesis assumes that herring growth is density-dependent because of intraspecific competition. Because cod is the main piscivore in the Baltic Sea (Rudstam et al. 1994), the collapse of the cod popula-

Received 31 January 2003. Accepted 30 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 19 March 2003.
J17317

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 doi: 10.1139/F03-167 © 2004 NRC Canada

tion in the 1980s removed a large portion of the predation pressure on herring (Nissling and Westin 1991). During the two past decades, the cod stock is believed to have been too low to influence herring abundance in the Gulf of Finland.

Other studies demonstrated that significant changes in herring food composition and feeding conditions have occurred in the northern Baltic Sea (e.g., Raid and Lankov 1995; Flinkman et al. 1998; Möllmann et al. 2000). During the years of low growth, herring consumed smaller plankton and the energy content of stomachs decreased (Flinkman et al. 1998). As a result of declining salinity in the Baltic Sea, the abundance of small plankton species, especially that of cladocerans, increased, while copepod abundance declined (Viitasalo et al. 1995). Also, Lankov and Kukk (2002) reported that since the end of the 1980s, the proportion of mysids and amphipods in the diet of Gulf of Finland herring has decreased. Because herring feed selectively on large-sized prey species (Sandström 1980; Flinkman et al. 1992), changes in food composition might have impacted negatively on herring feeding conditions and, hence, growth. According to this bottom-up hypothesis, herring would encounter energetically less valuable food in the low salinity conditions. In this case, it is not necessary to assume density-dependence of Baltic herring growth.

One of the most crucial questions on herring fisheries management concerns the effect of fishing pressure on Baltic herring growth. If the population density limits herring growth, the herring will grow better if fishing pressure is increased. If density does not limit herring growth, increased fishing pressure will not improve growth. Instead, a too intense fishery might destabilize the herring stock and cause a collapse of the population.

The aim of this study was to investigate which environmental factors affect Baltic herring growth. For this purpose, we used the longest time series available on Baltic herring growth, collected by the Estonian Marine Institute since the 1950s. The data were analysed against a set of background variables, including hydrography, zooplankton, as well as predators and competitors of Baltic herring. We used zooplankton data of the Estonian Marine Institute for 1961–1995 to describe food availability for Baltic herring.

We hypothesized that if a density-dependent mechanism affected herring growth, herring WAA should correlate negatively with herring numbers. Also, if herring growth was limited by the total availability of food for herring, a negative correlation between herring biomass and zooplankton abundance should be evident. However, if food quality regulated herring growth (i.e., a density-independent mechanism), a change in herring WAA might correspond with changes in zooplankton species composition.

Materials and methods

Herring weight-at-age

The age-specific herring weight data from the Gulf of Finland, sampled and treated by Estonian Marine Institute, were applied. Regular random samples (approximately 100 herrings) have been collected from trapnet catches during spawning time (one to two samples per 5-day period) and trawl catches (three to six samples a month) at the same coastal stations, one in the western and another in the eastern part of the Gulf. The samples from trawl catches were taken year-round during the ice-free period. Annually 10 000 – 20 000 herrings were examined for age and weight. Averaged yearly WAAs were applied for calculations and, for simplicity of the presentation, an average was calculated for weights of 1- and 2-, 3- and 4-, 5- and 6-, and 7- and 8-year-old herring.

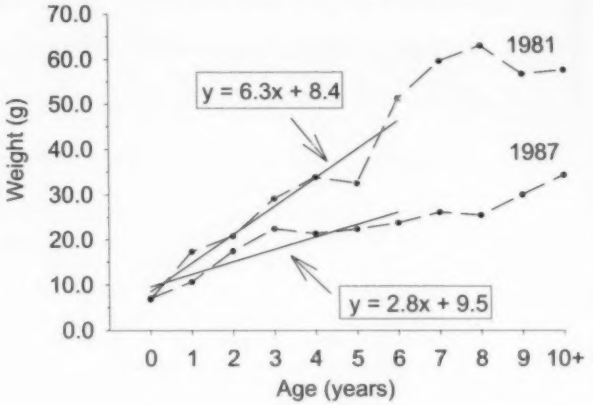

Fig. 1. Herring (*Clupea harengus membras*) weight plotted against herring age. Two examples are shown for determining the growth k (i.e., slope) for the year classes 1981 and 1987. Slope was determined by using a linear model ($y = kx + b$).

The growth rates for herring year classes were determined as follows: the weight of each year class was plotted against age, and the slope of the regression was determined assuming a linear relationship between age and weight (Fig. 1). Ages 0–6 were used for the regression because the growth was judged to be sufficiently linear during these years. Also, growth increment for ages 0–8 was determined to analyse the annual effects on growth. The growth increment for each year and each year class were determined by subtracting the weight of herrings during each year from their weight a year later.

Background data

Salinity and temperature

The data were obtained from the database of the Finnish Institute of Marine Research and were collected at three stations in the Gulf of Finland: Harmaja (years 1950–1993), Tvärminne (years 1950–1999), and Utö (years 1950–1999, except 1972–1980) (Fig. 2). The locations of the stations represent herring feeding and overwintering areas in the Gulf of Finland (Sjöblom 1961). The samples were taken approximately 36 times·year^{-1} from Tvärminne and Harmaja and 19 times·year^{-1} from Utö. The samples were collected with a "Ruttner"-type water sampler equipped with a thermometer (Ruttner 1963, p. 26). Salinity was determined by the Knudsen's method (Knudsen 1903) in 1950–1964 and with a salinometer in 1965–2000.

The salinity and temperature data were processed as follows. First, the average of 0-, 5-, 10-, 20-, and 30-m depths for each station was determined. Then the annual average and finally the average among all three stations was calculated. The average for the years of missing data was esti-

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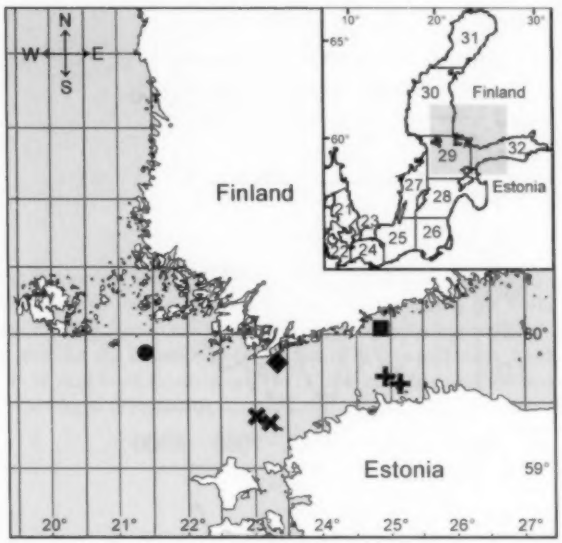
Fig. 2. Study area in the Baltic Sea, showing International Council for the Exploration of the Sea (ICES) subdivisions 21–32 and sampling stations for salinity and temperature (Harmaja (■), Tvärminne (◆), Utö (●)) and zooplankton (stations 17 and 18 (+), stations 22 and 23 (×)).



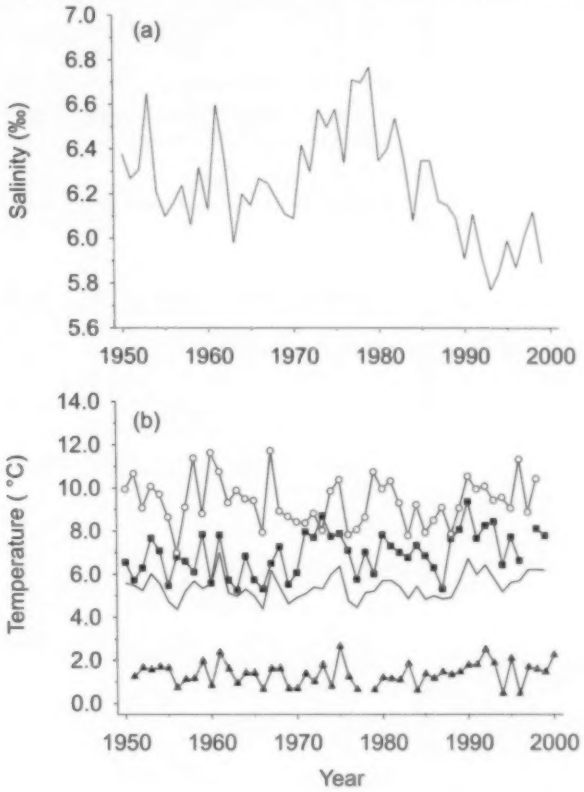
mated from the difference between the three-station mean and the two-station mean (determined for the years when data were available for all stations). After averaging, the temperature data were divided into three periods: December–April, May–July, and August–November, hereafter called winter, summer, and autumn periods, respectively. The latter two correspond roughly to periods when water temperature was increasing and decreasing, respectively.

Zooplankton

The samples have been collected from four (>70 m depth) pelagic stations located in the Gulf of Finland (Fig. 2) between 1963 and 1992 by using a 170-μm mesh net (Lumberg and Ojaveer 1991). During that time, vertical hauls were taken between 0 and10 m, 10 and 25 m, 25 and 50 m, and 50 m to bottom. After 1992, the samples were collected by using a 90-μm mesh net and vertical hauls were taken from bottom to the surface. As a rule, samples were taken three times a year: in May, August, and October–November. The plankton was identified to species level whenever possible, and copepods were further classified to sex and developmental stage (Lumberg and Ojaveer 1991). However, we consider only the total number of adults and copepodite stages I–V in this paper.

For the annual averages, stations 17 and 18 (Fig. 2) were compared with a *t* test to find out if it was feasible to use values from only one station when the data were missing from the other station. The data were first logarithmic transformed ($\log_{10}(x + 1)$) to normalize the data. The same was done with stations 22 and 23. The tests indicated no significant difference, and thus values from one station were used in a few cases. The annual averages were determined for the eastern and western stations from logarithmic values to reduce variance among spring, summer, and autumn values.

Fig. 3. Annual averages of surface water (0–30 m) (*a*) salinity and (*b*) temperature at Utö, Tvärminne, and Harmaja in the years 1950–1999. Seasonal averages of temperature (May–July (■), August–November (○), and December–April (▲)) are shown in (*b*).



For the correlation analysis, an average was calculated between the eastern and western stations. Copepod nauplii and rotifers were excluded from the analysis because the change in the net mesh size in 1992 may have influenced the amount of small plankters in the sample. Also, species that were rare or were not assumed to be important food for herring (*Cercopagis pengoi*, *Harpacticoida*, *Ceriodaphnia quadrangula*, *Daphnia cucullata*, *Leptodora kindtii*, *Chydorus sphaericus*, *Fritillaria borealis*, and *Balanus improvisus*) were not considered here. Biomass was calculated as carbon content by multiplying plankton abundances with individual carbon contents (Flinkman et al. 1998; Pellikka and Viljamaa 1998).

Herring, sprat, and cod stocks

To examine changes in fish stocks, we used data compiled by ICES (International Council for the Exploration of the Sea) (ICES 2000). We used data from ICES subdivisions 25–29 and 32 for herring, 22–32 for sprat, and 25–32 for cod (Fig. 2), because there were no estimates available on fish stocks specifically for the Gulf of Finland for the whole period considered in this study.

Statistical analysis

All data were tested for normal distributions. Pearson product moment correlation coefficients were calculated among the

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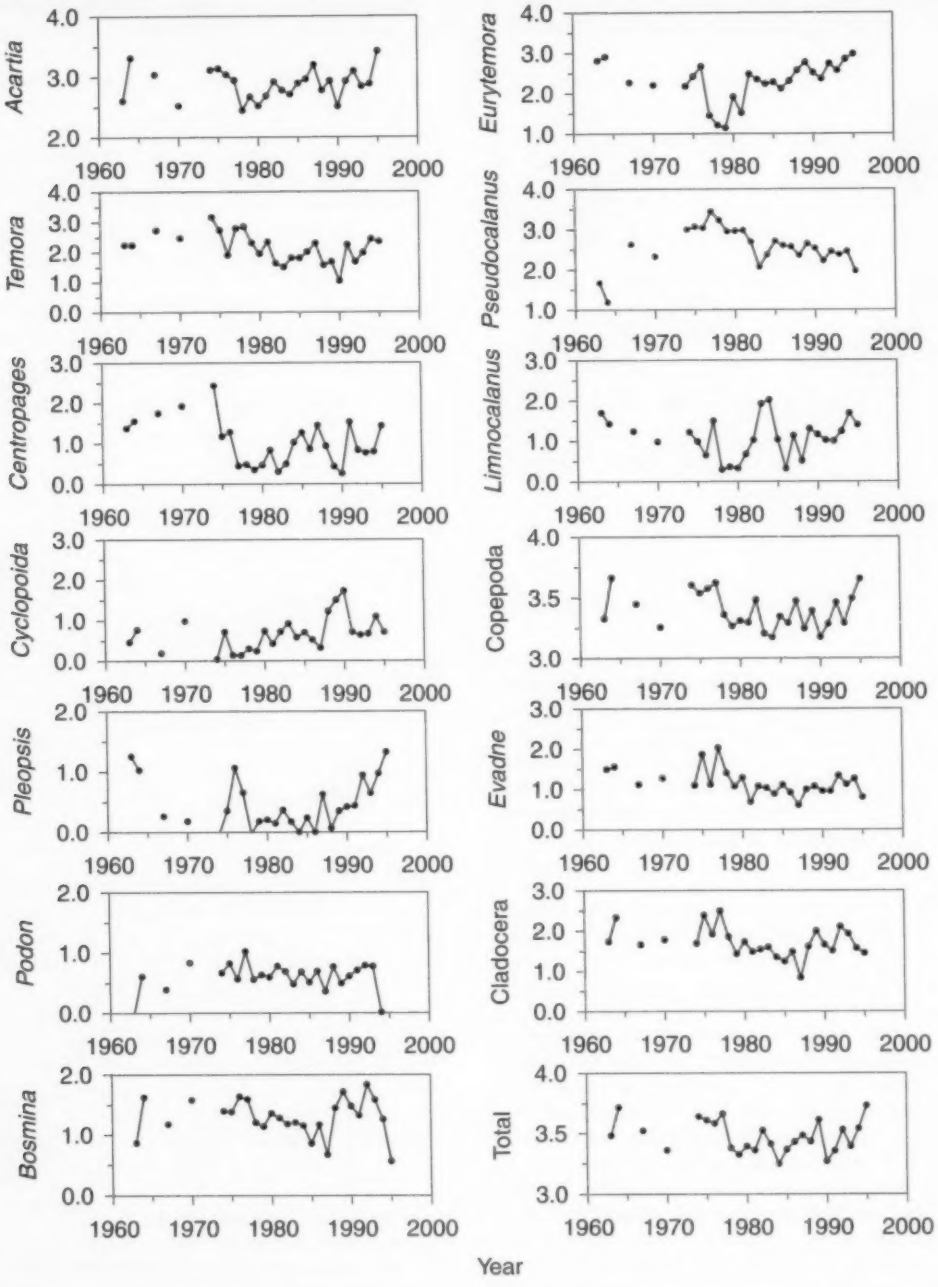
Fig. 4. Annual averages for zooplankton abundance ($\log_{10}$ individuals·m^{-3}) in the Gulf of Finland at stations 17, 18, 22, and 23 in 1963–1995. Note different scales on *y* axes.



herring WAA, weight increment for the year, annual salinity and temperature, zooplankton species abundance and biomass, and fish stocks (herring density and biomass, sprat and cod biomass). Also, Pearson product moment correlation coefficients were calculated between herring growth rate and 6-year moving average of salinity, temperature, and fish stocks data. For the *p* values, Bonferroni-adjusted probabilities were determined. The possible time lags among WAA, salinity, and herring abundance were determined by calculating cross correlation functions with the statistical package Systat 8.0. Because the main trend of salinity in the Gulf of Finland was similar with that in the Baltic Proper (Anonymous 1996), we considered it reasonable to compare salinity and fish stocks data even though they originated from different areas.

Redundancy analysis (RDA) and correlation plot were used to summarize the major patterns in the data and to visualize

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Table 1. Pearson's correlation coefficients among herring weight-at-age (WAA); herring total abundance (Herrab); cod, sprat, and herring biomass; salinity (*S*), and temperature (*T*) in the years 1974–1999 ($n = 26$).

				Biomass		
	T	*S*	Herrab	Herring	Sprat	Cod
WAA 1–2	–0.46	0.83***	0.59	0.95***	–0.75***	0.74**
WAA 3–4	–0.51	0.77***	0.50	0.87***	–0.80***	0.90***
WAA 5–6	–0.54	0.66*	0.41	0.72**	–0.82***	0.87***
WAA 7–8	–0.54	0.45	0.21	0.52	–0.82***	0.64*
Cod	0.45	0.70*	0.44	0.72**	–0.68*	—
S	–0.43	—	0.37	0.81***	–0.66*	0.70*

Note: *, $0.01 < p < 0.05$; **, $0.001 < p < 0.01$; ***, $p < 0.001$.

Fig. 5. Herring (*Clupea harengus membras*) biomass (●) and abundance (◇) and cod (○) and sprat (▼) biomass in the Baltic Sea. Herring stock data have been compiled from International Council for the Exploration of the Sea (ICES) subdivisions 25–29 and 32, cod from subdivisions 25–32, and sprat from subdivisions 22–32 (from ICES 2000).

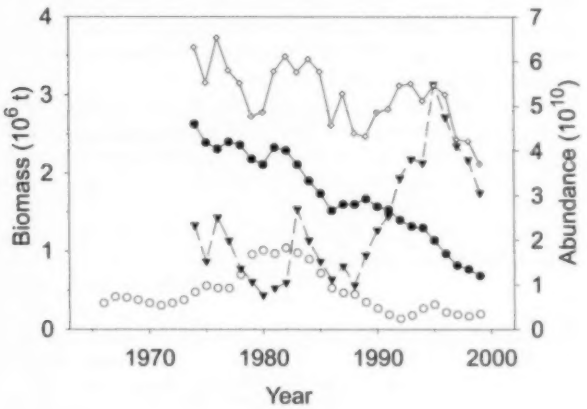
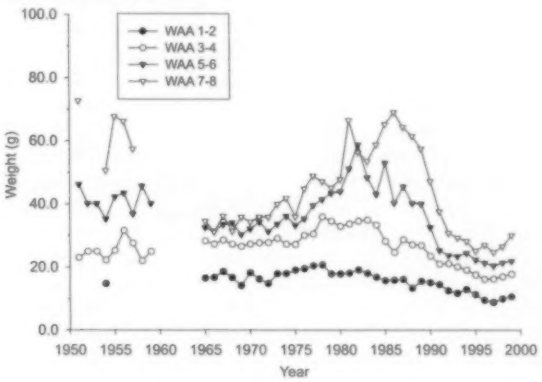


Fig. 6. Herring (*Clupea harengus membras*) weight-at-age (WAA) in the Gulf of Finland. Averages are estimated between WAAs 1 and 2; 3 and 4; 5 and 6; and 7 and 8. No data were available for the years 1960–1964. WAA data in the 1950s originates predominantly from spawning concentrations; therefore, WAAs before and after 1964 are not fully comparable.



connections between herring WAA and the most important environmental factors. Only years 1974–1995 were used in the RDA because missing values are not allowed in the analysis. RDA is the linear method of direct ordination (ter Braak 1994). In the correlation plot, acute angles between vectors indicate high positive correlation and length of vector indicates how strongly the variable is related to the displayed ordination (ter Braak 1994). Arrows point in the direction of increasing value, and by perpendicularly projecting points of each environmental variable (salinity, temperature, fish stocks, and zooplankton data) onto WAA arrows (WAA treated in the analysis as species data), an approximate ranking of correlations can be obtained. Also, the environmental arrows form by themselves a plot of correlations among environmental variables. Sample years form a plot of fitted abundance with WAA and environmental variables, and ranking of the values can be obtained by projection. How well the data are displayed is expressed by the percent variance accounted for and this can be derived from the sum of eigenvalues (ter Braak 1994). All ordinations were performed using the Canoco for Windows 4.0 package.

Results

Salinity and temperature in the Gulf of Finland

Salinity has been highest during 1973–1982 in the Gulf of Finland (Fig. 3*a*). After that, salinity has been decreasing. Other peaks in salinity have occurred in the years 1953 and 1961. The annual average temperature did not show any trend, but the summer temperature (May–July) increased during the research period (Pearson's correlation coefficient $r = 0.47$, $p < 0.001$, $n = 50$; Fig. 3*b*).

Zooplankton in the Gulf of Finland

Significant variations have occurred in abundances of mesozooplankton species in the 1960s–1990s (Fig. 4). Of the most abundant species, *Temora longicornis*, *Centropages hamatus*, and *Pseudocalanus minutus elongatus* decreased during 1970s and 1980s, whereas *Eurytemora affinis*, cyclopoids, and *Pleopsis polyphemoides* (Cladocera) have increased since the late 1970s. The total mesozooplankton abundance suitable for herring was generally lowest in the 1980s.

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Fig. 7. Weights of Baltic herring (*Clupea harengus membras*) year classes (*a*) at 5-year intervals from 1965 to 1990 and (*b*) in the 1980s. The year class 1973 is also shown in (*a*) as an example of highly accelerated growth.

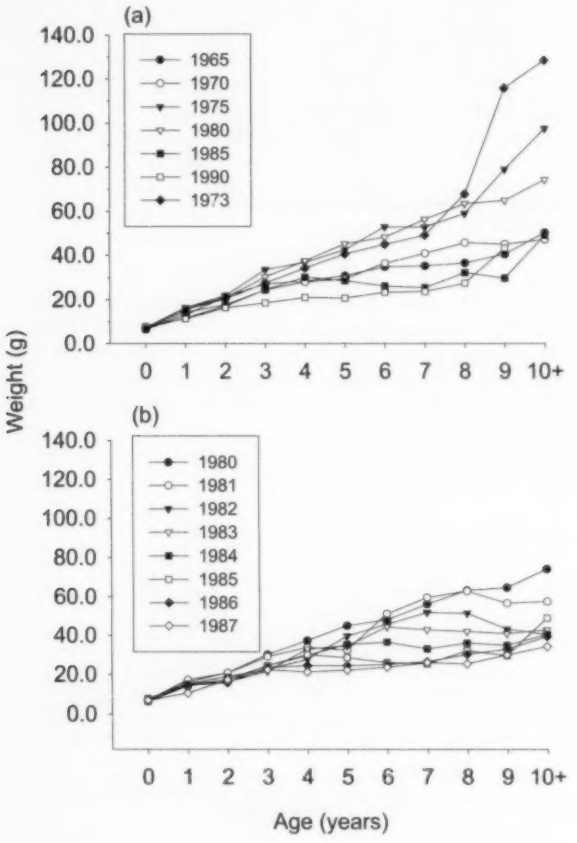


Table 2. Pearson's correlation coefficients among herring growth rate (GR) and 6-year moving average of herring total abundance (Herrab); cod, sprat, and herring biomass; salinity (*S*); and temperature (*T*) in the years 1965–1966 and 1970–1993 ($n = 20$).

				Biomass		
	T	*S*	Herrab	Herring	Sprat	Cod
GR	–0.77**	0.91***	0.79**	0.90***	–0.72*	0.93***

Note: *, $0.01 < p < 0.05$; **, $0.001 < p < 0.01$; ***, $p < 0.001$.

Herring, sprat and cod stocks in the Baltic Sea

The biomass of Baltic herring stock has decreased almost continuously since the 1970s (Fig. 5). However, herring abundance has not changed in the same way, although the general trend has also been decreasing. Herring abundance was the highest in 1974–1978, 1981–1985, and 1992–1996. During the years 1996–1999, the abundance of herring stock has decreased by more than 30%. Cod biomass began declining in the 1980s and has been at historic low levels in the 1990s. Sprat biomass started to increase in late 1980s and peaked in 1995. The correlation between cod and sprat biomass was negative, whereas herring abundance correlated positively with cod biomass. Further, herring and cod biomass correlated positively with salinity, whereas the correlation between sprat biomass and salinity was negative (Table 1).

Fig. 8. Growth rate (*k*) of Baltic herring (*Clupea harengus membras*) year classes plotted against salinity in the Gulf of Finland. Linear regression line has been added.

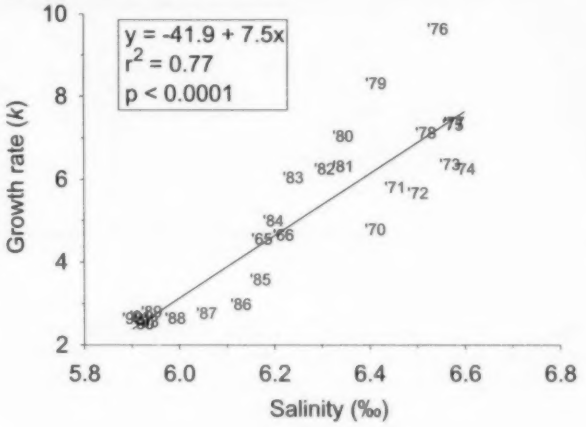
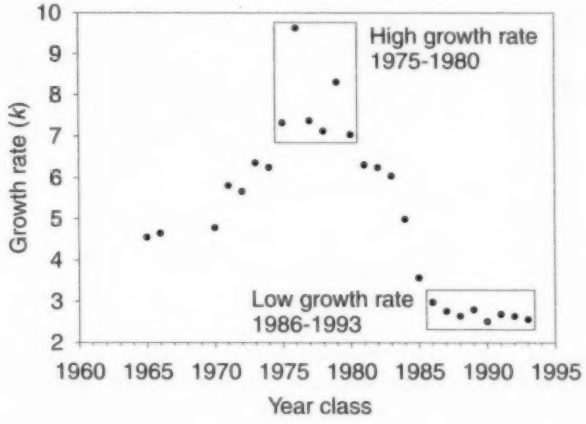


Fig. 9. Growth rates (*k*) of Baltic herring (*Clupea harengus membras*) year classes. Highest (1975–1980) and lowest (1986–93) growth rates are shown in boxes. The average zooplankton biomass structure during these years is shown in Fig. 10.



Herring WAA in the Gulf of Finland

During the last 50 years, herring WAA fluctuated remarkably in the Gulf of Finland, especially in the older age groups (Fig. 6). For example, the average WAA for the 7- to 8-year-old herring was 69 g in 1986 but only 27 g 10 years later. At the end of the 1970s, the herring WAA started to increase, staying high during the 1980s. In the early 1990s, the herring WAA decreased rapidly, reaching its lowest point in all age groups in 1996–1997. In 1998–1999, herring WAA increased slightly again.

It must be noted that the material collected in the 1950s originated predominantly from spawning concentrations, be-

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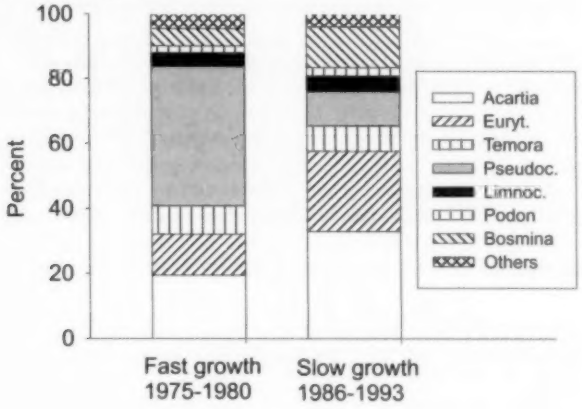
Fig. 10. Zooplankton biomass structure (in percent of carbon content) in the Gulf of Finland during high (1975–1980) and low (1986–1993) growth rate (cf. Fig. 9). Acartia, *Acartia* spp.; Euryt., *Eurytemora affinis*; Temora, *Temora longicornis*; Pseudoc., *Pseudocalanus minutus elongatus*; Limnoc, *Limnocalanus macrurus*; Podon, *Podon intermedius*; Bosmina, *Bosmina longispina maritima*; Others, *Centropages hamatus*, Cyclopoida, *Pleopsis polyphemoides*, and *Evadne nordmanni*.



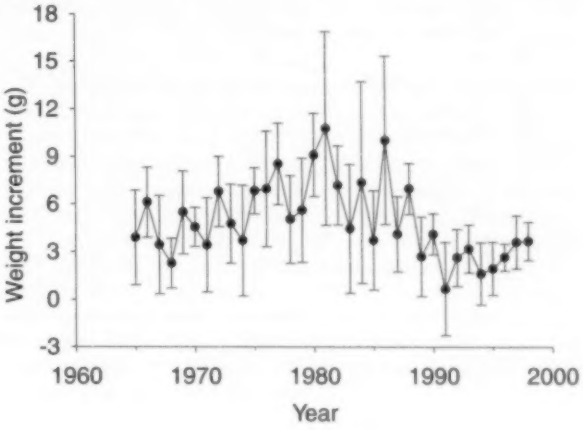
cause Estonia had no trawl fishery in the Gulf of Finland at that time. Because herring caught on spawning grounds is usually larger than corresponding age groups in trawl catches, the WAAs before and after 1960 are not fully comparable. This might explain higher weight of 5- to 8-year-old herring in the 1950s than in the 1960s and the 1970s. However, 3- to 4-year-old herring were smaller in the 1950s than in the next few decades.

Growth rates of the year- classes and weight increment for the year

The year classes hatched in 1965 and every 5years after were chosen to illustrate the growth of the year classes in different decades in the Gulf of Finland (Fig. 7*a*). In addition, the year class 1973 was chosen to represent an example of highly accelerated growth after age 8. The growth accelerated also in the year class 1975. The fast-growing year classes (1973, 1975, and 1980) differed from the slow-growing ones as early as 3 years old and remained larger also later. A closer look was taken at the year classes hatched during the 1980s, because during that time herring WAA changed the most (Fig. 7*b*). In the 1980s, every year class grew slower than the one hatched a year earlier. In fact, the growth of the year classes hatched during 1981–1986 almost ceased during 1989. The analysis on the slopes of the growth rates (k) of year classes 1965–1966 and 1970–1993 showed a positive relationship between k and 6-year average of salinity ($r^2 = 0.77$, $p < 0.0001$; Fig. 8). Growth rate also correlated positively with 6-year average of herring abundance and cod biomass (Table 2). In contrast, correlations between growth rate and temperature and between growth rate and sprat biomass were negative.

We show the growth rates of herring year classes plotted against the year (Fig. 9). Carbon content of the zooplankton community during the years of fast growth (1975–1980) was compared with that during the years of slow growth (1986–1993). The total average biomasses of the mesozooplankton communities for the two time periods were 3.84 mg C·m^{-3} and 4.56 mg C·m^{-3}, respectively. An evident difference between the two time periods was in the proportion of *Pseudocalanus minutus elongatus*,which represented 43% of the total zooplankton carbon content in the years of high growth but only 11% when herring growth was slow (Fig. 10). During the years of slow growth, the share of *Acartia* spp., *Eurytemora affinis*, and *Bosmina longispina maritima* increased mostly at the expense at *Pseudocalanus minutus elongatus*.

Fig. 11. Average weight increment for Baltic herring (*Clupea harengus membras*) ages 0–6. Error bars shown are standard deviations.



Average weight increment for ages 0–6 have more or less similar trend as herring WAA have in the Gulf of Finland (Fig. 11). There were no significant correlations between the year-class weight increment and zooplankton species abundances or biomass. Total biomass of herring correlated positively with weight increment of 0- to 1-year-olds ($r = 0.71$, $0.01 < p < 0.05$, $n = 24$), and correlation was negative between weight increment of 2- to 3-year-olds and sprat biomass ($r = -0.66$, $0.01 < p < 0.05$, $n = 24$). Weight increment was also plotted against salinity, and analysis showed a significant positive relationship between salinity and weight increment for ages 0–5 (Fig. 12).

Relationships between herring WAA and the background data

The WAAs of 1- to 6-year-old herring correlated positively with salinity (Table 1). Correlation between WAA and salinity was even higher with a 2- to 4-year time lag, except in 1- to 2-year-old herring, which correlated most significantly with salinity without any time lag. Cod biomass correlated positively with WAAs, also with various time lags, whereas correlation with sprat biomass was negative. There was no significant correlation between WAA and herring total abundance.

As for zooplankton, the only species with a significant positive correlation with herring WAA and biomass was the copepod *Pseudocalanus minutus elongatus* ($r = 0.77$, $0.001 < p < 0.01$ for both WAA 1–2 and herring biomass, $n = 22$). The abundance of other zooplankton species correlated in-

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Fig. 12. Baltic herring (*Clupea harengus membras*) weight increment for the year in the Gulf of Finland plotted against salinity. Linear regression lines have been added.

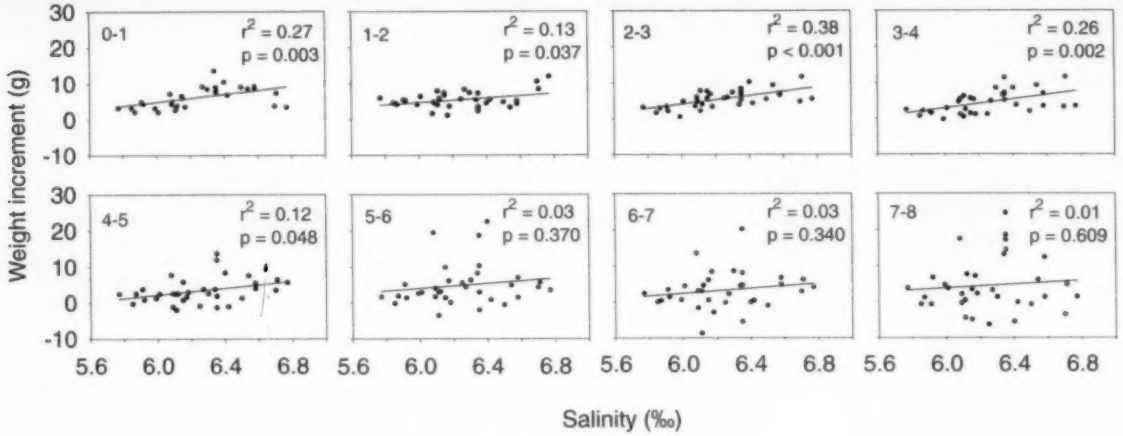
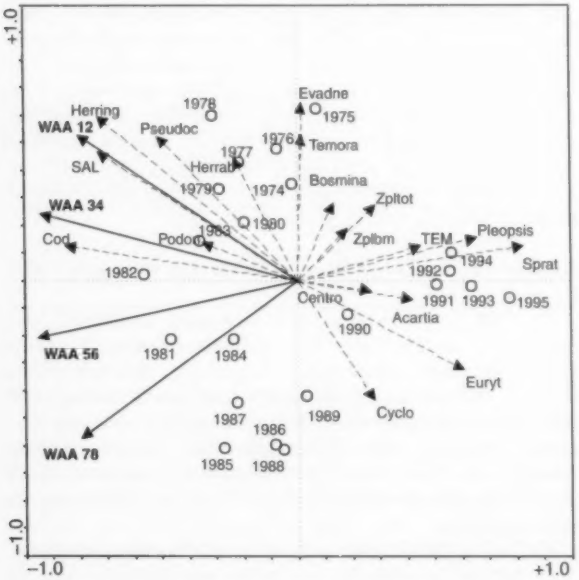


Fig. 13. Correlation plot of the redundancy analysis (RDA) on the relationship between herring (*Clupea harengus membras*) WAA (weight-at-age) (solid lines) and environmental variables (dashed lines). Sample years are also shown (○). Correlation plot displays 93.5% of the variance in the WAA. Eigenvalues of the first three axes are 0.76, 0.18, and 0.02. Herrab, herring total abundance; Sprat, sprat biomass; Cod, cod biomass; Herring, herring biomass; SAL, salinity; TEM, temperature; Zplbm, zooplankton biomass; Zpltot, zooplankton total abundance; Acartia, *Acartia* spp.; Euryt, *Eurytemora affinis*; Temora, *Temora longicornis*; Pseudoc, *Pseudocalanus minutus elongatus*; Podon, *Podon intermedius*; Bosmina, *Bosmina longispina maritima*; Centro, *Centropages hamatus*; Cyclo, cyclopoida; Pleopsis, *Pleopsis polyphemoides*; Evadne, *Evadne nordmanni*.



significantly with herring WAA. Zooplankton total abundance and biomass did not correlate with herring biomass or WAA.

In the RDA, the first two axes explained 93.5% of total variance in the herring WAA (first axis, *x*: 75.9%, second axis, *y*: 17.6%). The third and fourth axes are not further discussed because of their low eigenvalues (λ_3 = 0.02, λ_4 = 0.02). The diagram (Fig. 13) shows high positive correlation between salinity and the weight of 1- to 4-year-old herring. Also, the WAAs of the younger stages were positively related to cod biomass and herring abundance, as well as abundances of *Pseudocalanus minutus elongatus*. The WAAs of the older year-classes (5–8) were most positively correlated with cod biomass and negatively with sprat biomass – WAA of the year classes 5–6 also with salinity; other strong relationships were not found (Table 1).

According to the RDA, *Pseudocalanus minutus elongatus* was positively related and *Eurytemora affinis* and *Acartia* spp. negatively related with salinity. In contrast, *Acartia* spp. and the cladocerans *Bosmina longispina maritima* and *Pleopsis polyphemoides* were most strongly (positively) related with temperature (Fig. 13).

Years are also plotted (Fig. 13) to indicate how the background variables have changed during the study period. For example, during the years 1991–1995 (which are positioned on the right-hand side of the plot), temperature, sprat biomass, and abundances of *Acartia* spp., and *Pleopsis polyphemoides* were higher than during the years 1981–1984 (which are found on the opposite side of the plot).

Discussion

There are a number of papers documenting density-dependent growth in herring in the different sea areas. Anthony and Fogarty (1985) noted a negative relationship between the length-at-age of 2-year-old Atlantic herring in the Gulf of Maine region and year-class abundance, which suggests a density-dependent control of growth. Tanasichuk (1997) also found a negative relationship between the size of 3-year-old Pacific herring and parental biomass. Results

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from the Baltic Sea are contradictory or cannot give a conclusive answer. For example, a significant positive correlation between the weight increments of younger herring age groups and the biomass of planktonic food was found in the Gulf of Riga and the northeast Baltic Proper (Ojaveer 1988, 1998), whereas Rudstam et al. (1994) and Möllmann and Köster (1999) did not find evidence for zooplankton abundance limiting herring growth in the Central Baltic. This may reflect differences in the conditions in various parts of the sea.

The density-dependence hypothesis assumes that herring growth declines when there are too many herring for the whole population to be sustained. Therefore, one would expect that (1) zooplankton biomass should decline during the herring population maximum and (2) Baltic herring growth is negatively correlated with herring abundance. Furthermore, if a top-down mechanism (reduced predation by cod) induced the herring stock increase, then (3) herring abundance should correlate negatively with the size of the cod stocks.

Our analyses showed that there was no significant correlation between total zooplankton abundance (or biomass) and herring biomass, WAA, or weight increment for the year. Also, WAAs of the 1- to 6-year-old herring, as well as weight increment, were not significantly correlated with herring abundance. Instead, herring growth (k) had a significant positive relationship with herring abundance. Further, there was no significant correlation between cod biomass and herring abundance. Thus, the assumptions suggesting a density-dependent control of herring growth in the Gulf of Finland were not supported by the data. However, because the herring stock data originate from the whole Baltic Sea, while the WAA data only represent the Gulf of Finland, conclusions on density dependency of herring growth need to be made cautiously. On the other hand, observed changes in WAA are not limited to one population, but represent a larger phenomenon, because similar changes in WAA have also been observed in other areas of the Baltic Sea (e.g., ICES 2000) and also in Finnish data that originate from the coastal Gulf of Finland, Gulf of Bothnia, and the northern Baltic Proper (Parmanne and Setälä 1996). Further, the Gulf of Finland and northern Baltic Proper are not hydrodynamically or topographically separated from the main basin of the Baltic Sea, and therefore the environmental conditions are very much similar. Also, there is no barrier for migrations of fish populations between these areas.

The failure to find correlation between Baltic herring and zooplankton stocks has long been a matter of debate: herring and sprat have been estimated to consume a large proportion of the annual zooplankton production (e.g., Arrhenius and Hansson 1993), but only little evidence for antagonism between the two parameters has been found. The answer may lie in prey-switching behaviour by herring (e.g., Lankov and Kukk 2002), as well as in the fact that zooplankton abundance varies far more rapidly than growth and population variations of herring. Also, patchy distribution of both herring and zooplankton may complicate the analysis of connections between them. Furthermore, some copepod eggs survive the digestive tract of herrings (cf., Flinkman et al. 1994), and the predation effect on the egg-carrying copepods may therefore be smaller than estimated. On the other hand, it is possible that top-down control between herring and their prey occurs during short time intervals, e.g., during the autumn decline of zooplankton (cf., Rudstam et al. 1992; Möllmann and Köster 1999) or locally, in large fish aggregations (Ojaveer et al. 1998).

Furthermore, the coupling between cod and herring stocks may not be tight: because of weak density effects on reproduction, clupeids have a great natural fluctuation in population size even without predation (Blaxter and Hunter 1982). Presently, the effect of cod can only be marginal in the Gulf of Finland because of their low abundance at present. However, cod predation may affect the sprat stock more strongly than it affects the herring stock. This is because sprat remains suitable size prey for cod during its whole life span, whereas herring grows out of the Baltic cod's range for prey size (Sparholt 1996). Therefore, the collapse of the cod stock in 1982–1992 might have caused the observed increase in the sprat stock in 1988–1995.

To summarize, herring growth in the Gulf of Finland was probably not limited by herring density and total quantity of zooplankton, but may have been limited by the availability of suitable type of plankters (as suggested by Flinkman et al. 1998) or by other energetically valuable food animals (mysids, amphipods; Lankov and Kukk 2002). When herring have grown well, the large-sized *Pseudocalanus minutus elongatus* has been the dominating species both in the zooplankton and in the herring diet (Raid and Lankov 1995; Möllmann and Köster 1999). In the present study, the WAA of the 1- to 2-year-old herring correlated most significantly with the abundance of *Pseudocalanus minutus elongatus*, which may indicate a great importance of this copepod species for the younger herring (cf., Lumberg and Ojaveer 1991). The reason that there is no effect for older herring is that the growth is determined by the first few years of life. During the period of slow growth, the proportions of *Acartia* spp., *E. affinis*, and *B. longispina* were greater. *Acartia* spp. is a small species and *E. affinis* shows strong escape responses (Viitasalo et al. 2001) and may therefore be difficult prey for herring. The decrease in the biomass of *Pseudocalanus minutus elongatus* and an increase of the share of *B. longispina*, *Acartia* spp., and *E. affinis* may have impacted herring feeding conditions negatively during the low salinity period.

It has also been suggested that the size-selective predation of cod on herring might explain a part of the positive correlation between cod biomass and herring WAA (Sparholt and Jensen 1992). Because cod predation mortality is greater for smaller clupeids, relatively more small-sized (younger or slow-growing) herring will be consumed when cod abundance is high (Sparholt and Jensen 1992). It is estimated that 20% of the variation in WAA was due to selective predation of cod in the southern Baltic Sea (Sparholt and Jensen 1992). However, cod predation on herring cannot explain all the changes in herring WAA in the Gulf of Finland, because herring became larger even before the cod appearance in this gulf (Raid 1995).

Although our results do not support the theory of intraspecific competition, competition for food might occur between herring and sprat, the other abundant clupeid in the Baltic Sea. The negative correlation among herring weight,

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growth rate, and sprat biomass supports this hypothesis. Sprat biomass has significantly increased after the collapse of the cod population and, if food amount is limiting, we can expect lower growth in sprat. Sprat WAA did not change much during 1970–1989, but after the 1990s, sprat WAA has decreased by 40% (International Council for the Exploration of the Sea 2000). The recent changes in the prey of herring, which increasingly overlaps with that of sprat, has probably increased food competition between these pelagic species, particularly during the present high abundance of sprat (Raid et al. 2003).

Stratification of the water column can also play an important role affecting the distribution of herring prey (Anonymous 1994). For example, mysid shrimps were more sparse during the years of weak stratification (late 1980s and 1990s) (e.g., Raid 1997). In contrast, in the periods of strong stratification, large concentrations of mysids occurring near the halocline may have generated good feeding opportunities for herring.

In conclusion, our results showed that in the Gulf of Finland, (1) herring WAA and the year-class growth rates correlated positively with salinity, and (2) WAA correlated positively with the abundance of the marine zooplankton species *Pseudocalanus minutus elongatus*. (3) A density-dependent mechanism was not likely to explain the changes in herring WAA in the Gulf of Finland, because we did not find evidence for the total amount of zooplankton limiting herring growth, and no significant correlation between herring WAAs and herring abundance could be found. Also, the growth rate correlated positively with herring abundance. However, firm conclusions on the density dependency of herring growth cannot be made. Instead, (4) competition for food might occur with sprat. In addition, (5) cod biomass positively correlated WAAs of different age herring, suggesting a common factor driving all these variables. Finally, (6) the zooplankton community structure changed during the research period, which supports the theory of a bottom-up controlling mechanism.

In the Baltic Sea, many ecological factors and variables seem to correlate with water salinity (cf., Segerstråle 1969). The changes in salinity are connected to exchange of water between the North Sea and the Baltic Sea. The influx of saline water increases not only the salinity of the Baltic Sea, but also the oxygen content of deeper water layers and the vertical mixing, promoting higher biological production and better growth of herring (Ojaveer and Lehtonen 2001). However, correlations do not prove cause–effect relationships between variables but merely show a synchronism of trends. Therefore, the most reliable conclusion arising from our data is that herring in the Gulf of Finland grows better during the phase of high salinity. The data do not reveal if this salinity effect is direct or indirect: the direct physiological impacts of salinity on Baltic herring growth are not known. However, whatever the mechanism is, this correlation may give a possibility for the prediction of herring growth in the Baltic Sea, since it has been suggested that the salinity level of the Baltic Sea can be predicted from climatic trends (Hänninen et al. 2000).

Acknowledgements

We thank Pekka Alenius (Finnish Institute of Marine Research) for salinity and temperature data. Comments on the manuscript by J. Engström-Öst, M. Lehtiniemi, R.W. Tanasichuck, and one anonymous reviewer are gratefully acknowledged. This research has been supported by the Walter and Andrée de Nottbeck Foundation, University of Helsinki, and the Academy of Finland.

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Changes in blood testosterone and progesterone concentrations of the North Atlantic minke whale (*Balaenoptera acutorostrata*) during the feeding season

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Abstract: An opportunity to study seasonal changes of sex hormones in the North Atlantic minke whale (common minke whale, *Balaenoptera acutorostrata*) arose when we obtained access to fresh postmortem blood samples from 104 females and 83 males. The whales were caught in the North Atlantic during May–September 1992–1995. Serum progesterone (P) and testosterone (T) concentrations were measured and compared with anatomical data. The frequency distribution of female serum P values showed two clusters, one consisting mainly of immature animals and the second of pregnant ones, with mean serum values of about 0.49 ± 0.04 (SE) and 44.2 ± 2.84 nmol·L^{-1}, respectively. The frequency distribution of male serum T did not show any group-specific distribution during the hunting season. The mean serum T value for the males was 0.63 ± 0.13 nmol·L^{-1}. Contrary to earlier reports on the Antarctic minke whale (*Balaenoptera bonaerensis*), serum T values rose during the hunting season in mature males ($p < 0.0001$). Serum P values in immature females increased during the season ($p = 0.015$). This increase agrees with the predominantly annual reproduction cycle of minke whales. Blood sex hormone measurements seem to be useful for detecting cyclic changes and pregnancy of minke whales.

Résumé : L'accès à des échantillons de sang frais prélevés après la mort chez 104 femelles et 83 mâles du petit rorqual commun (*Balaenoptera acutorostrata*) nous a fourni l'occasion d'étudier les changements saisonniers des hormones sexuelles chez les petits rorquals de l'Atlantique-Nord. Les rorquals ont été capturés dans l'Atlantique-Nord de mai à septembre, en 1992–1995. Nous avons mesuré les concentrations de progestérone (P) et de testostérone (T) sériques et noté les caractéristiques anatomiques correspondantes. La distribution de fréquence des concentrations de P sérique chez les femelles indique deux regroupements, l'un correspondant surtout à des animaux immatures et le second à des femelles enceintes, avec des valeurs moyennes respectives d'environ 0,49 (± 0,04, erreur standard (SE)) nmol·L^{-1} et 44,2 (± 2,84) nmol·L^{-1}. La distribution des fréquences des concentrations de T sérique chez les mâles n'indique pas de répartition particulière pour un groupe ou un autre pendant la saison de la chasse : la valeur moyenne est de 0,63 ± 0,13) nmol·L^{-1}. Contrairement à ce qu'on a signalé antérieurement chez des petits rorquals de l'Antarctique (*Balaenoptera bonaerensis*), les concentrations de T sérique augmentent durant la saison de la chasse chez les mâles matures ($p < 0,0001$). Les concentrations de P sérique augmentent chez les femelles immatures ($p = 0,015$) durant la saison. Cet accroissement correspond au cycle de reproduction surtout annuel des petits rorquals. La détermination des hormones sexuelles du sang semble donc être utile pour détecter les changements cycliques et la grossesse chez les petits rorquals.

[Traduit par la Rédaction]

Received 17 December 2002. Accepted 28 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 22 March 2004.
J17245

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 doi: 10.1139/F03-159 © 2004 NRC Canada

Introduction

The North Atlantic minke whale (*Balaenoptera acutorostrata*) species (the International Whaling Commission recommends the name "common minke whale", which will be used hereafter in this article) is one of the smallest in size of the genus *Balaenoptera*, which belongs to the Balaenopteridae family. As reviewed recently (Lockyer 1984, 1999; Horwood 1990), a considerable body of knowledge has been gathered by pioneering studies mainly during the last 40–50 years on the reproduction of the common minke whale. Contrary to other baleen whales, which generally reproduce every second year or even less frequently, the evidence available at present indicates that the common minke whale has mostly a yearly reproductive cycle. Apparent pregnancy rates (proportion of sexually mature females with fetuses, females with calves not included) between 90% and 100% of caught common minke whales have persistently been reported (Christensen 1981; Sigurjónsson 1995). This is about 50% higher than in the northern fin whale (*Balaenoptera physalus*) (Martin 1982; Lockyer and Sigurjónsson 1991) and sei whale (*Balaenoptera borealis*) (Lockyer and Martin 1983). Likewise, the ovulation rates (number of corpora counted in ovaries per year by age) have generally been reported to be about 90% and higher, which is roughly two times greater than those for fin and sei whales (Horwood 1990; Lockyer 1999).

The common minke whale, like most of the other baleen whales, has an annual migration cycle of feeding, which should be in step with its breeding cycle. The animals breed at lower and warmer latitudes but go to colder areas in the north during the summer for feeding. Gestation period is 10 months, a month or two shorter than for the other baleen whales, and the suckling period is thought to be less than 6 months (Lockyer 1999). Many lactating female minke whales have been found to be ovulating as evidenced by corpora lutea in their ovaries (International Whaling Commission 1979), and it seems probable that they do conceive while being suckled. If conception occurred mainly before the middle of the suckling period, the minke cows could maintain an annual reproduction cycle that fitted into their yearly migration. The postpartum inhibition of ovulation during suckling is variable in different animals but seems to be mainly controlled by the suckling frequency of the offspring (McNeilly 1994), which causes suppression of the pulsatile secretion of gonadotropin-releasing hormone. Progesterone (P) and the endogenous opioid system are probably involved (Soaje et al. 2002), but the exact mechanism at the hypothalamic level is not yet clear.

The yearly reproductive cycle of common minke whales with increased ovulation and pregnancy rates, i.e., increased ovarian activity, should be reflected in different serum P concentrations when compared with other rorquals with a 2-year cycle. This comparison applies to the North Atlantic fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003) in both of which serum P concentrations have been measured.

Antarctic minke whales caught off Durban, South Africa, during the winter months were reported to have higher mean testicular weights per length than those taken in the Antarctic during the summer months (Best 1982). However, no definite seasonal variation in serum testosterone (T) or P concentrations has so far been found in either sex of the Antarctic minke whale during the months of December–March (Yoshioka and Fujise 1992; Iga et al. 1996; Mogoe et al. 2000). Using heterologous antisera, Suzuki et al. (2001) also studied the concentrations of gonadotropins in the pituitary of the Antarctic minke whale during the months of December–March and found no rise in luteinizing hormone values and a significant rise in follicle stimulating hormone values only from February to March. However, serum T and P concentrations were mostly undectable in immature males as well as mature males and immature females, respectively. This is contrary to our own findings for two other species of the same genus, the northern fin whale (Kjeld and Árnason 1990; Kjeld et al. 1992) and the sei whale (Kjeld et al. 2003), both of which showed significant increases of serum T concentrations during the hunting season.

Here, using relatively sensitive radioimmunoassays, we report our serum T and P measurements on samples available from the common minke whale. The frequency distributions of the serum values are presented and the concentrations related to the time of the season, the length of the animals, and their anatomically assessed sexual status.

Materials and methods

Collection and storage of samples

The whales were caught off Lofoten and Vesterålen (15 females and 27 males) and off Finnmark (17 females and 20 males), both northern Norway, off the coast of the Kola Peninsula, Russia (eight females and seven males), and off the coast of Bear Island (23 females and 27 males) and Spitsbergen (41 females and two males), both Svalbard, Norway, during the period May–September 1992–1995. The whales were caught for scientific purposes and a few papers have already been published based on this material alone or related common minke whale material (Haug et al. 1995; Nordoy 1995; Tryland et al. 1999). Blood samples were collected by cutting into the jugular vein immediately after the animals had been taken aboard the vessel, generally less than 40 min postmortem. Blood was left to coagulate in the vacutainers for 40–50 min and then centrifuged and serum separated and kept at –20 °C.

Radioimmunoassays

Serum T was measured by a modified radioimmunoassay method described by Kjeld et al. (2003) using a more sensitive and specific antiserum (rabbit anti-T-19; Cat. No. 20-TR05; Fitzgerald Industries International, Inc., Concord, Mass.). The antiserum had cross-reactivity of 1.0% for dihydrotestosterone, <1.0% for nortestosterone, <0.02% for P, and <0.01% for other steroids tested. The assay had an interassay imprecision (coefficient of variation) of 10% for a sample of 3.1 nmol·L^{-1} and an intraassay imprecision of 8% for a sample of 1.4 nmol·L^{-1}. The detection limit of the assay was 0.05 nmol·L^{-1}.

Serum P was measured by a modified radioimmunoassay method described by Kjeld et al. (1980, 1992). By using a more sensitive and specific antiserum (rabbit anti-P-11; Cat. No. 20-PR20; Fitzgerald Industries International, Inc.), the

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Table 1. Female common minke whales classified into reproductive groups (I, II, and III) by the specific serum progesterone (P) distribution.

		Serum P ($nmol \cdot L^{-1}$)		Length (m)	
Group P limits ($nmol \cdot L^{-1}$)	n	Mean (SE)	Range	Mean (SE)	Range
I: $P \leq 2.5$	58	0.49 (0.04)	0.05–2.23	6.64 (0.10)	4.85–8.00
II: $2.5 < P < 6.0$	6	4.30 (0.56)	2.83–5.69	6.82 (0.30)	5.55–7.45
III: $P \geq 6.0$	40	44.23(2.84)	6.71–90.85	7.90 (0.07)[a]	6.70–9.00

Note: The number (n) in each group and mean (SE) and range of serum P values and body length are given. All P-value means in groups are significantly different ($p < 0.0001$) from each other.

[a]Significantly different ($p < 0.001$) from the mean value just above.

chromatography steps could be omitted. The antiserum used had a cross-reactivity of <1.0% for 17-hydroxyprogesterone, <1.0% for pregnenolone, <1.0% for cortisol, <1.0% for 11-deoxycorticosterone, and 0.0% for androstenedione. After addition of an internal tritiated P standard to each of the 0.5-mL serum samples, they were extracted in eight volumes of petroleum ether (boiling range 40–80 °C) (Merck). Mean intra- and inter-assay imprecision (coefficient of variation) was 7% ($n = 8$) and 10% ($n = 11$), respectively, for a serum control sample with a P concentration of 4.8 $nmol \cdot L^{-1}$. The detection limit of the assay was 0.03 $nmol \cdot L^{-1}$. Results were corrected by the recovery of the internal standard, which averaged 85%. Conversion factors for the hormones from SI units to conventional (older) units are as follows: T, $nmol \cdot L^{-1} \times 0.288 = ng \cdot mL^{-1}$; P, $nmol \cdot L^{-1} \times 0.315 = ng \cdot mL^{-1}$.

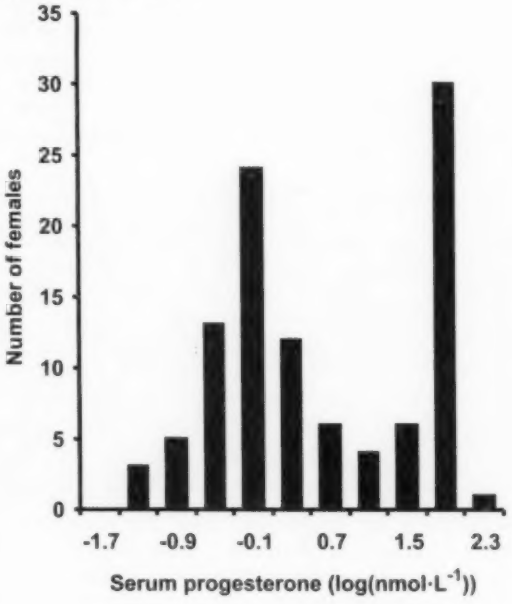
Gross anatomical studies

Before the hormonal measurements, the reproductive status of the females (immature, mature resting, pregnant, ovulating) was evaluated by studying the anatomy of the internal sex organs. In 96 of the 104 females, this was accomplished by looking for a fetus or either corpora lutea or corpora albicantia or both in the ovaries and by an examination of the uterine cornua width. Based on a previous study (Christensen 1981) of body length related to anatomic measures of the genital organs of both sexes of the whales, their reproductive status could also be estimated. This study showed that 50% of the females and males were sexually mature when they had reached a length of 7.15 and 6.75 m, respectively, and that approximately 70% of either sex became mature within a body length interval ranging 0.35 m above and below the respective means cited above (Christensen 1981). Here, this is used as an indicator of sexual maturity in the males, separating the mature from the immature bulls.

Statistics

A t test was used to compare groups by their means. An association between variables was assessed by the Pearson or Kendall correlation. Linear regression analysis was used to estimate the geometric mean serum hormone values as dependent on the time of hunting season. Means are presented with their standard error if used for comparison. For description of the data, the number of observations, ranges, means, and standard deviations are presented. The level of significance was set at 0.05. For the figures included herein, the $\log_{10}$-transformed concentrations of serum P and T are given because the hormone levels had a near-normal distribution after being transformed to logarithmic values (Armitage and Berry 1987).

Fig. 1. Frequency distribution of $\log_{10}$-transformed serum progesterone (P) concentrations of 104 female common minke whales. Two clusters of values are clearly seen, one with a peak between $\log_{10}$ P = –0.5 and –0.1 (0.32 and 0.79 $nmol \cdot L^{-1}$) and the second between $\log_{10}$ P = 1.5 and 1.9 (31.6 and 79.4 $nmol \cdot L^{-1}$), i.e., about two orders of magnitude apart. The numbers on the horizontal axis refer to the right end of the respective intervals (bins), each 0.4 in width.



Results

The mean (SD) length of all of the animals ($n = 187$) was 7.26 (0.92) m (range 4.82–9.0 m) with no significant difference between sexes or between the five different hunting regions. Only 10 females and eight males were <6 m in body length. There was no significant difference between the $\log_{10}$-transformed means of serum T or P values of comparable reproductive groups of whales from the different regions.

Females

Serum P concentrations were measured in 104 female minke whales. Two clusterings of values can be seen, one

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Table 2. Female common minke whales classified into reproductive groups by anatomical indicators.

		Serum P (nmol·L^{-1})		Length (m)	
Reproductive group	*n*	Mean (SE)	Range	Mean (SE)	Range
Immature	51	1.62 (0.83)	0.05–43.9	6.56 (0.09)	4.85–7.65
Resting	2	0.32 (0.10)	0.22–0.41	7.34 (0.12)	7.22–7.46
Ovulating	9	18.6 (7.4)[a]	0.22–52.2	7.79 (0.07)[b]	7.48–8.10
Pregnant	34	44.0 (3.5)[a]	2.83–90.6	7.92 (0.08)[b]	6.70–9.00

Note: The number (*n*) in each group and mean (SE) and range of serum progesterone (P) values and body length are given.

[a]Significantly different ($p < 0.01$) from the mean value just above.

[b]Significantlydifferent ($p < 0.001$) from the mean length of immature females.

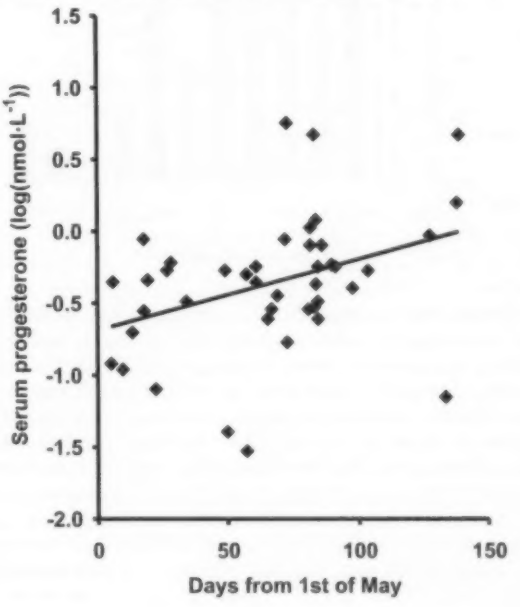
around a concentration of 0.50 nmol·L^{-1} ($\log_{10}$ P = –0.3) and the second around a concentration of 45 nmol·L^{-1} ($\log_{10}$ P = 1.65) (Fig. 1).

For separating the serum P concentrations into groups, the limiting P values (Table 1) were somewhat arbitrarily chosen after visual inspection of the serum P's frequency distribution with different bin ranges (P-value intervals in histograms). The 58 females with P below 2.5 nmol·L^{-1} ($\log_{10}$ P = 0.4) constitute a P-specific population, 84% of which consisted of immature and resting females when classified by anatomical data. The group with the highest serum P values (group III) was given the preliminary lower limit of 6.0 nmol·L^{-1} ($\log_{10}$ P = 0.8). This value was decided on after inspection of its P distribution and the fact that the three lowest fetus-confirmed pregnancies had P levels of 2.8, 6.7, and 9.9 nmol·L^{-1} and the three highest values without confirmed pregnancy were 4.8, 4.8, and 5.7 nmol·L^{-1}. The P levels of group III had a mean (SD) of 44.2 (18.0) nmol·L^{-1} (i.e., the 2.5% fractile is 4.1 nmol·L^{-1}, which may be compared with 6.0 nmol·L^{-1} chosen above), which is almost two orders of magnitude higher than the mean (0.49) for the cluster (group I) with the lowest P values. All females with fetuses, except one, had serum values belonging to group III, which consisted of 40 females, 33 with fetus (83%), four ovulating, one immature, and two undetermined as judged by anatomical data. In between the two groups of high and low P values were six females, referred to as group II, with intermediate serum P concentrations.

The body length of group III had a near-normal frequency distribution (data not shown) with a mean (SE) of 7.90 (0.07) m, which was greater ($p < 0.001$) than that of the intermediary group (group II), which in turn was greater than that of group I (immature plus resting), but not significantly (Table 1).

For comparison, the females were also classified on the basis of the anatomical indicators, dividing the cows into four reproductive groups: sexually immature, mature resting, mature ovulating, and mature pregnant (Table 2). The numbers in the different groups are similar in the two tables, but immature and mature resting animals are put into one group in Table 1 (P ≤ 2.5 nmol·L^{-1}), as the P levels do not separate them. The anatomical classification shows 51 immature, two resting, nine ovulating, and 34 pregnant cows. Of the 51 immature cows, 47 (92%) had P values below 2.5 nmol·L^{-1} and 33 (97%) of the 34 pregnant ones had serum P values above 6.0 nmol·L^{-1}. Nine cows, with an average body length of 7.79 m, had an ovarian corpus luteum without a fetus detected in the uterus, i.e., were classified as ovulating females by the anatomical data. Four of them had P values consistent with pregnancy levels, i.e., 23.4–52.2 nmol·L^{-1}, but the other five had P concentrations with a range of 0.19–2.19 nmol·L^{-1}. One cow, of 6.7 m with serum P levels of 43.9 nmol·L^{-1}, had been classified as immature by anatomical indicators. There was no anatomical classification for eight cows, which explains the difference of the total numbers of cows in Tables 1 and 2.

Fig. 2. The $\log_{10}$-transformed serum progesterone (P) concentrations of 43 female common minke whales, 90% immature by anatomical indicators, all shorter than 7.15 m, plotted against the days of catch of the summer season from 1 May. From the slope of the regression line $\log_{10}$ P = –0.69 + 0.005 days (R^2 = 14%, p = 0.015), the estimated relative change in the predicted geometric mean of the P values for every 10 days is $10^{0.05}$ = 1.12, i.e., a 12% increase (95% confidence interval 2–23%.).



The apparent pregnancy rate was 85% when the anatomically mature cows were counted against the ones with serum P values above 6.0 nmol·L^{-1}. The length of fetuses (range 1–150 cm) correlated positively with time of catch during the hunting season (n = 34, R^2 = 41%, $p < 0.0001$) but did not correlate with serum P levels.

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Fig. 3. Frequency distribution of $\log_{10}$-transformed serum testosterone (T) concentrations of 83 male common minke whales. The open bar at the left includes the 13 whales at the assay's detection limits. Concentrations were widely scattered with about 80% under $\log_{10}$ P = 0, i.e., P = 1.0 nmol·L^{-1}. Thirteen individuals had levels at or under the detection limits (0.05 nmol·L^{-1}) of the assay and three had levels higher than 5.0 nmol·L^{-1}. The numbers on the horizontal axis refer to the right end of the respective intervals (bins), each 0.2 in width.

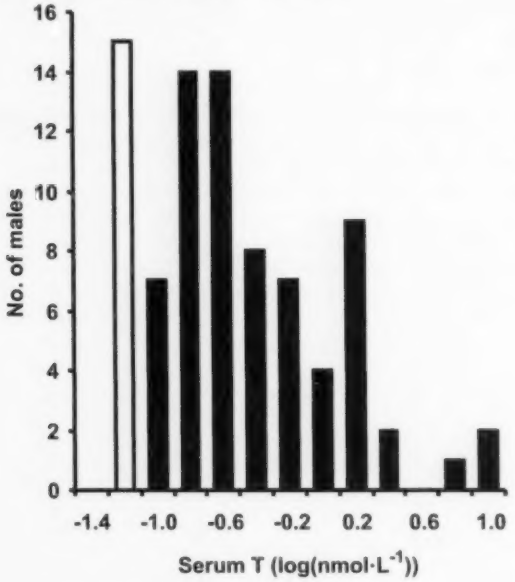
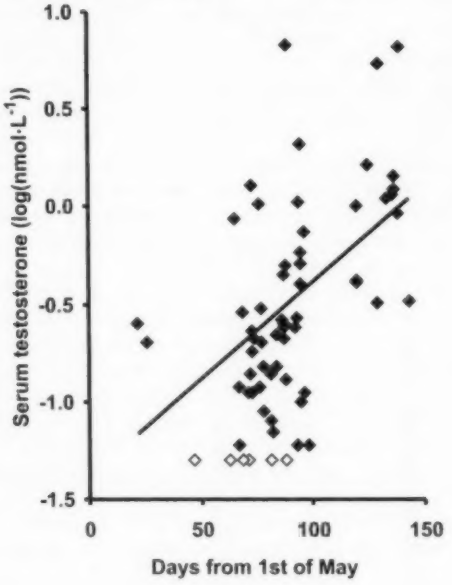


Fig. 4. The $\log_{10}$-transformed serum testosterone (T) levels of 58 male common minke whales longer than 6.75 m (sexually mature) plotted against days of catch of the summer season from May 1. From the slope of the regression line $\log_{10}$ T = –1.39 + 0.010 days (R^2 = 26%, $p < 0.0001$), the estimated relative change in the predicted geometric mean of the serum T values for every 10 days is $10^{0.1}$ = 1.26, i.e., a 26% increase (95% confidence interval 14–40%). Six values, indicated by open diamonds, at (or below) the detection limit of the assay are not included in the regression analysis.



Whereas the serum P levels in group III (>6.0 nmol·L^{-1}) did not change significantly with days of catch during the feeding season, the P levels in group I (<2.5 nmol·L^{-1}) were found to increase significantly (p = 0.026) during the summer months. Females shorter than 7.15 m, 90% of which had been classified as immature by anatomical methods, were therefore studied further in this respect. There was a significant increase in the serum levels with time (n = 43, R^2 = 14%, p = 0.015) (Fig. 2). The 6.7-m-long female mentioned above with serum P levels of 43.9 nmol·L^{-1} was considered pregnant and was not included in this regression analysis.

Males

Thirteen males had T concentrations at or below the detection limits (0.05 nmol·L^{-1}) of the assay. Seven of these animals were regarded as immature on the basis of their length (<6.75 m). The mean (SD) of the serum T values for all of the males measured above the detection limits (n = 70) was 0.63 (1.21) nmol·L^{-1} (range 0.06–6.75 nmol·L^{-1}). Three individuals, two of which were caught in September, had higher levels of serum T than the rest, i. e. 5.6, 6.6, and 6.9 nmol·L^{-1} (Fig. 3). Serum T values and body length for both immature (<6.75 m) and mature (≥6.75 m) males (maturity based on body length) did not correlate significantly. Mature males (n = 58), however, had higher mean T levels than the immature ones (n = 12), i.e., 0.73 and 0.28 nmol·L^{-1}, respectively, but the means were not significantly different (p = 0.24) (animals at or below detection limits not included). No correlation between body length and time of the hunting period was found in either group.

For the mature males (≥6.75 m), an increase of mean serum T values was found with days of catch ($p < 0.0001$) during the hunting season (Fig. 4). Six mature bulls, caught in the middle and earlier half of the season, had T values at or below the detection limit (0.05 nmol·L^{-1}) of the assay and were excluded from the regression analysis. These six males can be accounted for in this context, giving a total of 64 bulls, by using a nonparametric Kendall correlation to assess the relationship between serum T and the days of the season. By this method, a correlation coefficient of 0.41 ($p <$ 0.0001) was obtained. For immature animals (<6.75 m), no significant increase of T levels with time was found.

Discussion

The average length of the ("adult") Northeast Atlantic common minke whale has been reported to be 7.15 m (Jonsgard 1951), which is similar to the mean length of all of the whales in this study (7.26 m). The whales from the five different locations in our study did not differ in length. Furthermore, comparison of the mean sex hormone concentrations of animals from the different areas showed no significant difference between comparable reproductive groups. Our material is, however, biased, as the whalers tend to take

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large animals, and they do not take either calves or cows with calves. The immature animals might, therefore, have a tendency to be near maturity.

One of the interesting results of this study on the common minke whale is the clear rise of serum T levels during the feeding season in the sexually mature males and the weaker, but still significant, rise of serum P levels in the immature females. The female immature group, selected by length (<7.15 m), contained no mature cows as judged by anatomical indicators, but the rising tendency is still there even if the cutoff point is lowered to <6.8 m. These hormonal changes have not been found in the Antarctic minke whale, the species most extensively studied in this respect so far (Yoshioka et al. 1990; Yoshioka and Fujise 1992; Iga et al. 1996). No similar studies have been done before on the common minke whale, but a rise of T levels during the feeding season has been described in the northern fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003). Three reasons for the above discrepancy seem most likely. Firstly, our serum assays have lower detection limits than those used by the above cited Japanese scientists, three times lower limits for the T assay and five times lower for the P assay. Secondly, the Antarctic minke whale may have lower hormonal levels in its peripheral blood than the common minke whale, thus adding one more chacteristic to several already known to differ between the two whale species. The Antarctic whale is, for instance, larger (Lockyer 1999), has a white band on its flippers, and has different genetic constitution (Árnason and Gullberg 1994). Thirdly, and probably most likely, the reason may be a combination of the two factors just mentioned.

Another result of interest is the relatively high serum P levels in the immature and resting females (0.49 ± 0.04 nmol·L^{-1}), which are at least five times higher than those (≤0.1 nmol·L^{-1}) reported for the fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003) during the same time of the year and probably higher than the undetectable levels of the Antarctic minke whale (Iga et al. 1996; Suzuki et al. 2001). Higher P levels have, however, been found (0.96 nmol·L^{-1}) in the immature group of the Antarctic minke whale (Yoshioka et al. 1990; Yoshioka and Fujise 1992), but, as mentioned above, no changes in levels with time were reported. The P levels in the immature and a few resting common minke whales suggest greater ovarian acitivity than in the fin and sei whales, which have a 2-year reproductive cycle. Increased P levels with time may indicate a first-time ovulation of prepubertal females with only a small elevation in serum P levels (about 1.6 nmol·L^{-1}) as seen in suckled beef cows in their first ovulation after giving birth (Perry et al. 1991). More recently, it has become apparent by transrectal ultrasonography that ovarian follicular development in ruminants occurs in wave-like patterns where P levels have a definite modulating role (Adams 1999; Menchaca and Rubianes 2002). Anovulatory follicular waves are found in the prepubertal period as well as in pregnancy and the seasonal anestrus. Furthermore, P itself may have a role in initiating ovulation (Zalányi 2001), as a rise in peripheral P levels precedes the luteinizing hormone surge of ovulation. The small number of resting cows among the female minke whales in this study is in agreement with earlier results (Iga et al. 1996; Suzuki et al. 2001) on the Antarctic minke whale, further supporting the assumption of mostly yearly reproductive cycles.

Elevated P values were always found when a fetus was present in a female except in one case where the level was 2.9 nmol·L^{-1}, a level that belongs to the range of the ovulating or intermediary group (group II). The mean P levels for pregnant females found in our study are similar to those reported for the pregnant Antarctic minke whale (54–58.2 nmol·L^{-1}) (Yoshioka et al. 1990; Yoshioka and Fujise 1992) and to those found in pregnant fin whales off Iceland (50.2 nmol·L^{-1}) (Kjeld and Árnason 1990; Kjeld et al. 1992). They are, however, about two times higher than those reported for the Antarctic minke whale in more recent papers (13.7–21.3 nmol·L^{-1}) (Iga et al. 1996; Suzuki et al. 2001).

The discrepancies between the high P levels in the pregnancy range and the biological evidence for ovulation without conception in four cases might have been caused by small fetuses that were not detected or that were lost during the handling process. Conversely, the five females with evidence of a corpus luteum but low P levels (0.22–2.23 nmol·L^{-1}) may have ovulated or even aborted at some earlier time, as we do not have any data on the age of the corpora lutea. The question arises whether some nonpregnant ovulating females might have high enough P levels to be included in group III and therefore counted as pregnant. This is unlikely for several reasons. In many terrestrial mammal species (Niswender and Nett 1994), as well as in the captive killer whale (*Orcinus orca*) (Robeck et al. 1993) and bottlenose dolphin (*Tursiops truncatus*) (Kirby 1990), P concentrations are considerably higher in pregnancy than after ovulation. The P distribution curve for group III should, therefore, have shown negative skewness or trailing to the left had there been any number of ovulators with lower levels included. Ovulation of the mating season has not started, as the T levels of the mature males are still rising at the end of the season, but they generally reach a plateau before the mating season starts (Bronson and Heideman 1994). For the closely related fin whale, it has been shown that for the months of June and July, almost all of the corpora lutea found indicated pregnancy (Lockyer and Sigurjónsson 1991). Finally, Mansour et al. (2002) have recently studied postmortem P levels in common minke whales' blubber and found a very decisive difference in levels between pregnant (range 72.5–1441 nmol·g blubber^{-1}) and nonpregnant females (4.5–10.8 nmol·g blubber^{-1}). This study does in fact suggest the possibility of correlating sex hormone levels in serum and blubber and then measuring the hormone levels in blubber biopsies of free-ranging whales to predict their reproductive status.

Female whales with P values >6.0 nmol·L^{-1} do clearly belong to a population with high P values, the logarithm of which has a near-normal distribution, almost certainly a group of pregnant animals. When using the anatomical indicators, all females of 7.7 m body length or longer were sexually mature. About 42% of those between 7.3 and 7.7 m were mature. The length at which 50% of female comman minke whales are sexually mature was estimated to be 7.50 m for minke whales off West Greenland during 1979–1981 (Larsen 1984) and 7.15 m for minke whales in the Barents Sea during 1972–1977 (Christensen 1981). These

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estimates could vary with time and location, but our results seem to fall between the two cited above. A pregnancy rate of 85% was found when anatomical data were used to discriminate between sexually mature and immature animals and the P assay to decide on pregnancy. If only anatomical data were used, the rate would be 79%. Our results are similar to those of Larsen (1984) of 89%, but Christensen (1981) reported a 99% pregnancy rate, which would agree more with the longest animals in the present study. For the Antarctic minke whale, Yoshioka et al. (1990) found a rate of 95% and Kato (1982) reported an average rate of 89%. The pregnancy rates of mature female minke whales, therefore, seem higher than those of the fin whales, in which a larger percentage of nonpregnant mature females are found (Kjeld et al. 1992). This again is presumably related to the shorter 1-year reproductive cycle of the minke whale (Kato 1982; Horwood 1990) compared with the 2-year cycle of the fin whale (Lockyer 1984).

The serum T concentrations of the males were widely scattered. The mean overall T level (0.63 $nmol \cdot L^{-1}$) was lower than that of the fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003) off Iceland but evidently higher than the levels of the Antarctic minke whale (Yoshioka and Fujise 1992; Fukui et al. 1996; Suzuki et al. 2001) in which 40–100% of the T levels were reported undetectable during the months of December–March. Mogoe et al. (2000) even found a decrease in the weight of the testes in the Antarctic minke whale during the December–February period.

Mean serum T values in the mature males doubled each month and would be about 11 $nmol \cdot L^{-1}$ at the end of December. At that time, serum T levels should be much more clearly separated in mature versus immature males than has been found in this study. Days of peak conception for whales have been found by regression of the lengths of fetuses with time and its extrapolation backwards. For the common minke whale, February has been predicted to be the month of peak conception (Lockyer 1984). Present T values would seem to agree with that mating time. Thus, in captive bottlenose dolphins (Schroeder and Keller 1989) and seasonally breeding terrestrial herbivores (Bronson and Heideman 1994), serum T concentrations generally reach a peak or an elevated plateau before the rutting period starts and then the levels begin to fall during the rut. For fin and sei whales, the peak of conception has been estimated to occur a month or two earlier than for the common minke whale (Lockyer 1999).

It is concluded that sex hormone measurements are a valuable tool for studying reproductive aspects of baleen whales, and, contrary to earlier reports on the Antarctic minke whale, serum T and P levels in common minke whales do have changes during the feeding season in males and females, respectively. These changes and the increased ovarian activity indicated by comparatively high serum P levels in immature and a few nonpregnant mature cows would support the notion that the common minke whale has a predominantly annual reproductive cycle.

Acknowledgements

We wish to thank K. Loftsson for his encouragement and enthusiasm. The technical help of A. Theódórsdóttir is much appreciated. A grant from the Icelandic Research Council is acknowledged. The minke whale samples were collected during the Norvegian Marine Mammal Research Program (1988–1994) and its contributors and participants are acknowledged for making the serum samples available to us.

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Temperature and hunger mediate sablefish (*Anoplopoma fimbria*) feeding motivation: implications for stock assessment

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Abstract: Laboratory experiments were conducted to test the hypothesis that temperature (2–8 °C) and recent feeding history (1–6 days of food deprivation) influence feeding motivation and attacks on baits by adult sablefish (*Anoplopoma fimbria*). Activity level after introduction of a bait-related olfactory cue increased with increasing water temperature and food deprivation. Fish at the lowest temperature (2 °C) attacked and consumed fewer squid baits (33–71%) than those at higher temperatures (100% at 8 °C). Baits were frequently inspected or handled multiple times before consumption in low temperatures, and time to attack (seconds to >40 min), time to consume, and time to handle baits (2–20 s) all decreased significantly with increasing temperature, with some temperature × feeding history interactions. The total ration consumed increased (<1–8% of body weight) with increasing water temperature. The observed variability in activity and feeding motivation in sablefish may have a large impact on the effective area of baited gear but is rarely considered in stock assessment models. In particular, population sizes based upon baited gear surveys may be underestimated in conditions where temperature is low, natural prey density is high, or where other environmental variables reduce feeding motivation.

Résumé : Nous avons mené des expériences de laboratoire pour vérifier l'hypothèse selon laquelle la température (2–8 °C) et l'alimentation récente (privation de nourriture durant 1–6 jours) influencent la motivation à s'alimenter et l'attaque d'appâts chez la morue charbonnière (*Anoplopoma fimbria*) adulte. Après l'introduction d'un signal olfactif relié à l'appât, le niveau d'activité augmente en fonction de la température et de la privation de nourriture. Les poissons attaquent et consomment moins des calmars utilisés comme appâts (33–71 %) à la température la plus basse (2 °C) qu'à une température plus élevée (100 % à 8 °C). Les appâts sont inspectés fréquemment ou touchés à plusieurs reprises avant d'être consommés aux températures basses; les temps requis pour l'attaque (quelques secondes à >40 min), la consommation et la manipulation (2–20 s) décroissent tous significativement à mesure que la température augmente; il y a aussi quelques effets croisés de la température × l'alimentation antérieure. La ration totale consommée augmente (<1–8 % de la masse du corps) en fonction de la température. La variabilité observée dans l'activité et la motivation à s'alimenter chez la morue charbonnière peut avoir un impact considérable sur la surface d'efficacité des engins de pêche munis d'appâts, cependant on en tient rarement compte dans les modèles d'évaluation des stocks. En particulier, les densités de populations basées sur des inventaires faits avec des engins de pêche munis d'appâts peuvent être sous-estimées lorsque les températures sont basses, les densités de proies naturelles élevées ou encore lorsque d'autres variables du milieu viennent réduire la motivation à manger.

[Traduit par la Rédaction]

Introduction

With ever-increasing pressure on limited fishery resources, there is an urgent need for improved stock assessments and more selective and efficient fishing methods to reduce the mortality of undersized and prohibited species. Traditional fisheries and stock assessment surveys that use hook and line gear or baited traps depend upon a fundamental knowledge of feeding behavior in the target species. Reports on the types of prey consumed, size relationships, daily food requirements, and variation in feeding with season for fishery resource species are widespread in the scientific literature, with many recent examples (Garrison 2000; Nielsen and Andersen 2001; Chase 2002). Also, artisanal, commercial, and recreational fishermen have a basic understanding of how environmental variables such as time of day, effect of currents, and natural occurrence of prey organisms affect fish feeding motivation (e.g., Johannes 1981; von Brandt

Received 10 February 2003. Accepted 11 December 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 29 March 2004.
J17329

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 doi: 10.1139/F03-170 © 2004 NRC Canada

1984; Fernö and Olsen 1994). In fact, any intrinsic (e.g., physiological) or extrinsic (environmental) parameter that affects feeding behavior and activity can have an important influence on the effectiveness of bait-dependent fishing gear (Engås and Løkkeborg 1994), but few experiments on these subjects have been designed and carried out, and the effects on stock size estimates are unknown.

Stock assessment with baited fishing gear is based upon assumptions related to the active space and effective area of each gear set (Engås and Løkkeborg 1994). Active space is the area or volume of water throughout which a chemical stimulus is present in concentrations that elicit detection and response by the fish of interest. Active space is determined by the release rate of feeding attractants from the bait and their transport through the water as well as the chemosensory thresholds in the target species. Laboratory experiments have shown that the olfactory thresholds of sablefish (*Anoplopoma fimbria*) vary with feeding history; consequently, active space varies greatly with the internal state of the fish (Løkkeborg et al. 1995). Effective area of the gear depends upon the motivation and ability of fish to locate, attack, and consume bait, but responsiveness to bait is usually unknown. In the few cases where data are available, fish that locate baits attack them with different frequencies depending upon fish species and size, time of day, season, and other factors (e.g., Løkkeborg 1994; Kaimmer 1999; Stoner 2003). Hence, fish catchability and effective area of the gear are variable, but this variability is rarely considered in stock assessment.

Sablefish are an important fishery resource in the north Pacific Ocean, with fishing grounds in deep continental slope waters from northern California to Alaska. Fishing is conducted primarily with longlines and a small amount of trawling, with a annual catch rate of ~15 000 tonnes and ex-vessel value of US$80 million in recent years in Alaska (National Marine Fisheries Service 1999). Highest sablefish abundance occurs at depths of 366–915 m (Hart 1973), and adult sablefish are known to occupy temperatures ranging from ~1.7 to 8.0 °C (D. Pearson, Southwest Fisheries Science Center, 110 Shaffer Road, Santa Cruz, CA 95060, U.S.A., and M. Schirripa, Northwest Fisheries Science Center, 2030 S. Marine Science Dr., Newport, OR 97365, U.S.A., personal communications). Sigler (2000) noted that the unknown extent to which water temperature and food availability affect the proportion of fish caught on longline gear is a "weak link" between catch rate and abundance estimates for sablefish. In this study, we test the hypothesis that feeding motivation and associated behavioral patterns in sablefish are related to water temperature and recent feeding history.

Materials and methods

Sablefish collection, rearing, and holding

Age-0 sablefish were captured in continental shelf waters off Newport, Oregon, using neuston nets in spring 1999 and reared at the Hatfield Marine Science Center. The young fish were held in circular tanks with a constant flow of seawater (10–12 °C) and transferred to progressively larger tanks (to 4.6 m in diameter and 1 m deep) with growth. For the first 2 months, the young fish were fed salmon pellets (Bio-Diet) ad libitum with automatic feeders, and for the next 10 months, they were fed to satiation three times per week. After 1 year, the sablefish were fed frozen squid (*Loligo opalescens*) twice per week to satiation. Long experience in our laboratory has shown that this feeding regimen provides for high growth rates and excellent health in sablefish (see Sogard and Olla 2001, 2002).

The entire population of sablefish was slowly acclimated to a holding temperature of 6 °C before experiments. This temperature is near the average temperature for large sablefish in the wild and provided a convenient point from which to acclimate fish for the experimental treatments, which ranged from 2 to 8 °C. The fish were fed whole squid twice weekly and held at 6 °C for at least 2 weeks before being moved into the experimental tanks. For the experiments, groups of three fish were measured to the nearest centimetre total length, weighed to the nearest 0.1 kg, and transferred to experimental tanks. Groups of three sablefish were used in the experiment because this is a schooling species, and they become disoriented and feed poorly when held individually. The sablefish ranged 56–72 cm and 1.3–2.7 kg at the beginning of the experiments. By the end of the experiments, weights ranged 2.8–3.7 kg. There was no significant difference in either lengths (analysis of variance (ANOVA), $p > 0.20$) or weights ($p > 0.45$) of fish tested in the three experimental temperatures, each of which was tested with an independent group of fish.

Experimental apparatus

Experimental groups were tested in six identical circular tanks (3 m in diameter, 1.2 m deep, 6360 L) supplied with seawater (250 $mL \cdot s^{-1}$) through a plastic elbow 15 cm from the bottom of each tank to create a circular flow. Water drained from the tanks via a 10-cm-diameter drain located 1 m above the tank floor. Lighting for the room was supplied from overhead fluorescent daylight bulbs with a 12 h dark – 12 h light cycle (13 μmol photons$\cdot m^{-2} \cdot s^{-1}$). Each tank was monitored with an overhead video camera mounted in the ceiling so that fish behavior could be recorded for later analysis. After the fish were transferred into the experimental tanks, water temperatures were adjusted at 1 $°C \cdot day^{-1}$ until experimental temperatures were reached. Temperature treatments were 2, 5, and 8 °C, spanning the natural distribution of adult sablefish. Fish were then allowed to acclimate to the experimental water temperature for 2 weeks before experiments were conducted. During the acclimation period, each tank was fed to a maximum of 8% of total fish wet weight in whole squid twice per week. The sablefish were given 1 h to consume the maximum ration, and then any remaining squid were removed and reweighed to determine the ration consumed. The 8% ration was selected after preliminary feeding trials showed that this was the amount consistently providing satiation in hungry fish. Larger rations can be consumed (≥10%) under certain circumstances, but this results in highly distended stomachs and regurgitation in some cases.

Experimental protocol

The experiments involved two variables: temperature and feeding history. A series of three feeding trials was conducted with each group of fish in each temperature using squid as the food stimulus. (Squid is the primary bait used

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for sablefish in the commercial longline fishery.) The first trial was run after a 6-day food deprivation period. Subsequently, runs were conducted after 3 days and 1 day of food deprivation. This fixed sequence of feeding trials resulted in a slightly longer temperature acclimation for the later trials; however, we expect that any difference in response would be minor compared with the large treatment effects observed in fish behavior. Also, this sequence of trials was necessary to keep the fish on a standard feeding schedule. For example, all of the fish would normally feed after 6 days of deprivation, but not necessarily after 1 day. Eight replicate feeding series were conducted with independent groups of sablefish for each of the three temperatures (72 fish in total). Temperature treatments were interspersed throughout the experimental period (March–October 2002) and among the six identical tanks.

Each feeding trial was initiated with the introduction of an olfactory cue. A squid extract was made following the procedure described by Løkkeborg et al. (1995). Briefly, 15 squid mantles were soaked and stirred in 15 L of chilled seawater for 30 min. The mantles were then removed and 75-mL aliquots of the supernatant were frozen at –20 °C and stored at –80 °C until needed.

On the day of an experiment, each tank was videotaped beginning at ~11:00. After 1 h, 50 mL of squid extract was injected into the saltwater supply line through a small line hanging below the top of the tank. During this time, the researchers remained below the top of the tanks so that they were not observed by the fish. Control injections of seawater revealed that the fish were undisturbed by the process. Trials with red dye showed that a scent injected into the system in this manner dispersed as a plume, making a complete circuit of the tank in 2 min. Ten minutes later, three whole squid (baits) averaging 50 g each were added to the tank at 30 s intervals via three feeding tubes (50-mm-diameter polyvinyl chloride pipe) separated by 60° of arc and ending 15 cm off the bottom. When all three baits were consumed, more squid were offered up to a total ration of 8% (including the baits). One hour after introduction of the first bait, any remaining squid were removed and weighed to calculate the total ration consumed. Videotaping continued until the end of the feeding period.

Behavioral analysis

Videotapes from each feeding trial were analyzed to provide an index of activity for fish in each tank before and after scent injection and to determine responses to each bait. An index was provided by counting the number of times fish crossed either of two lines (drawn on the video monitor) that divided the tank into quarters. Preliminary analysis revealed that the total number of line crossings during 4-min intervals before and after scent injection provided consistent indices for activity level. Activity typically increased with scent introduction and then decreased relatively quickly after 3–4 min. A second index of activity was estimated by counting line crossings for 2 min at 10-min intervals during the 1 h of video recording before the introduction of olfactory cues. This approach yielded results identical to the 4-min pre-cue index, and only the latter are reported here.

The videotapes were also used to determine sablefish behavior as they attacked the baits. The following behaviors were recorded. (*i*) Bait inspection: a fish changed course and approached the bait within a few centimetres but did not touch it, (*ii*) bait touch: a fish touched the bait with its snout but did not bite it, (*iii*) incomplete bite: some part of the bait was taken into the mouth then released, (*iv*) spit: the bait was ejected from the mouth, (*v*) complete bite: the fish's mouth was closed over the bait, and (*vi*) handling time: total time from initial bite in a sequence to a complete bite. Incomplete and complete bites were considered attacks on the bait but not bait inspections or touches. Timed observations were recorded for each bait beginning at time 0 when the bait emerged from the feeding tube. Analyses were concentrated on time to first bite, time to complete bite, handling time, and the proportions of baits attacked and consumed under each of the experimental conditions. Attack and consumption rates were each calculated as the proportion of the baits initially offered to each tank (three baits per tank). The total ration consumed was calculated for the entire feeding period, including all of the squid offered (not just the initial offering), and is reported as the percentage of fish wet weight for a tank of three fish.

Statistical analyses

Two forms of ANOVA were used in this investigation. Friedman's nonparametric ANOVA and multiple comparison (Conover 1980) was used to test for effects of food deprivation on activity and for several of the feeding responses (i.e., time to attack baits, time to consume baits, number of squid consumed, handling time). This approach was most appropriate because repeated measures were used to compare the three feeding periods and because some of the responses were truncated rather than measured directly. For example, squid bait was not always attacked and consumed during the 1-h videotape period but, given enough time, the bait would have been consumed. For analysis, a value of 60 min was assigned for attack time in trials where searches were made but location and attack did not occur during the feeding trial. Standard parametric one-way ANOVA was used to test for the effects of temperature when observations were independent (among different temperature treatments) and when the measurements were quantitative. This included comparison of activity, ration size, and bait handling times. ANOVA was followed with Tukey's multiple comparison.

Results

Activity and response to olfactory cues

Pre-cue activity levels were highest in fish living at the highest temperature (8 °C) (Fig. 1), but variation within each treatment was large and the effect of temperature was significant only for fish deprived of food for 6 days (Table 1). Pre-cue activity tended to increase with increasing food deprivation (Fig. 1), but differences were significant only in 8 °C water, where the mean activity index increased 34% between 1 day of food deprivation and 6 days.

Sablefish typically responded to the introduction of an olfactory cue with increased swimming speed and rates of turning. In most cases, these behavioral responses resulted in increased activity indices (Fig. 1). The effect of temperature on post-cue activity was significant for all three levels of food deprivation (Table 1), with the lowest activity at 2 °C.

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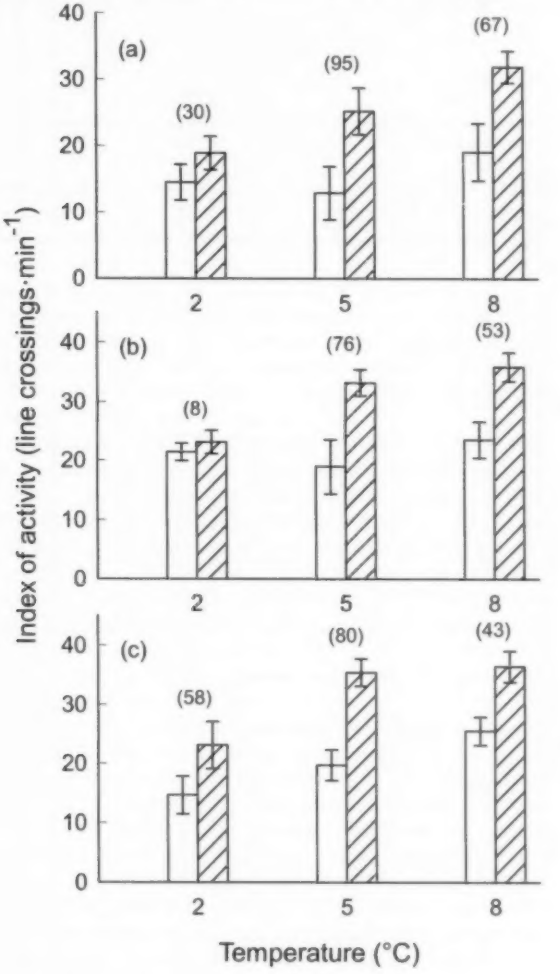
Fig. 1. Index of activity for sablefish in three different temperatures and at three levels of food deprivation: (*a*) 1 day, (*b*) 3 days, and (*c*) 6 days. Activity is shown before (open bars) and after (hatched bars) a standard olfactory cue was introduced into the experimental tank. Values are mean ± SE for the number of line crossings per minute in 4-min intervals before and after injection of the cue. Eight replicates were tested for each combination of temperature and food deprivation. Numbers over the histogram pairs represent the percent change in activity.



The effect of food deprivation was not significant for fish in 2 °C water but significant in both 5 and 8 °C water. Post-cue activity increased with food deprivation.

The percent change in activity between pre- and post-cue periods varied among both replicate tanks and the different treatments (Fig. 1). The greatest mean change in activity occurred in sablefish at 5 °C (76–95% increases) because pre-cue activity levels were relatively low and responses to squid odor were high, particularly in the fish with longer food deprivation. Fish in 8 °C water always had strong, positive responses to the olfactory cue, but their swimming speeds were generally high before the cue was introduced. Therefore, the overall difference in 8 °C water was lower than that in 5 °C water for all three food deprivation treatments. Fish at 2 °C had strong responses to the olfactory cue after 6 days of food deprivation (58%), but the response was weak (8%) after just 3 days. The average increase in activity in 2 °C fish deprived of food for 1 day was substantial (30%) because the fish were often motionless on the bottom of the tank before cue introduction in this treatment combination.

Table 1. Summary of statistical results for the effects of temperature and food deprivation on activity, total ration, and bait attack behavior of sablefish.

Behavioral measure	Data subset	ANOVA results (*p* value)	Multiple-range test
Effects of temperature			
Pre-cue activity	1 day	0.482	ns
	3 days	0.624	ns
	6 days	0.037	2 < 8
Post-cue activity	1 day	0.016	2 < 8
	3 days	0.001	2 < 5 = 8
	6 days	0.009	2 < 5 = 8
No. of baits consumed	1 day	0.021	2 < 5 = 8
	3 days	0.034	2 < 5 = 8
	6 days	0.223	ns
Total ration consumed	1 day	<0.001	2 < 5 < 8
	3 days	<0.001	2 < 5 < 8
	6 days	<0.001	2 < 5 < 8
Time to attack bait	1 day	<0.001	2 > 5 > 8
	3 days	<0.001	2 > 5 > 8
	6 days	<0.001	2 > 5 > 8
Time to consume bait	1 day	0.003	2 > 5 > 8
	3 days	0.002	2 > 5 = 8
	6 days	0.002	2 > 5 = 8
Bait handling time	1 day	0.001	2 > 5 > 8
	3 days	0.008	2 > 5 = 8
	6 days	0.027	2 > 5 = 8
Effects of food deprivation			
Pre-cue activity	2 °C	0.093	ns
	5 °C	0.14	ns
	8 °C	0.021	1 < 3 = 6
Post-cue activity	2 °C	0.417	ns
	5 °C	0.002	1 < 3 = 6
	8 °C	0.021	1 < 3 = 6
No. of baits consumed	2 °C	0.296	ns
	5 °C	0.430	ns
	8 °C	No variance	ns
Total ration consumed	2 °C	0.102	ns
	5 °C	0.009	1 < 3 = 6
	8 °C	0.197	ns
Time to attack bait	2 °C	0.552	ns
	5 °C	0.093	ns
	8 °C	0.223	ns
Time to consume bait	2 °C	0.911	ns
	5 °C	0.040	1 > 3 = 6
	8 °C	0.168	ns
Bait handling time	2 °C	0.472	ns
	5 °C	0.368	ns
	8 °C	0.911	ns

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Table 2. Summary of attack and consumption rates on squid baits by sablefish held in three different temperatures and with three periods of food deprivation.

	Food deprivation (days)		
Temperature (°C)	1	3	6
Attack rates			
2	50	62	83
5	88	100	100
8	100	100	100
Consumption rates			
2	33	46	71
5	79	100	100
8	100	100	100

Note: Values are the percentages of total numbers (n = 24) presented to fish in each treatment category.

However, variation was large and three tanks of fish under these conditions demonstrated no change in activity.

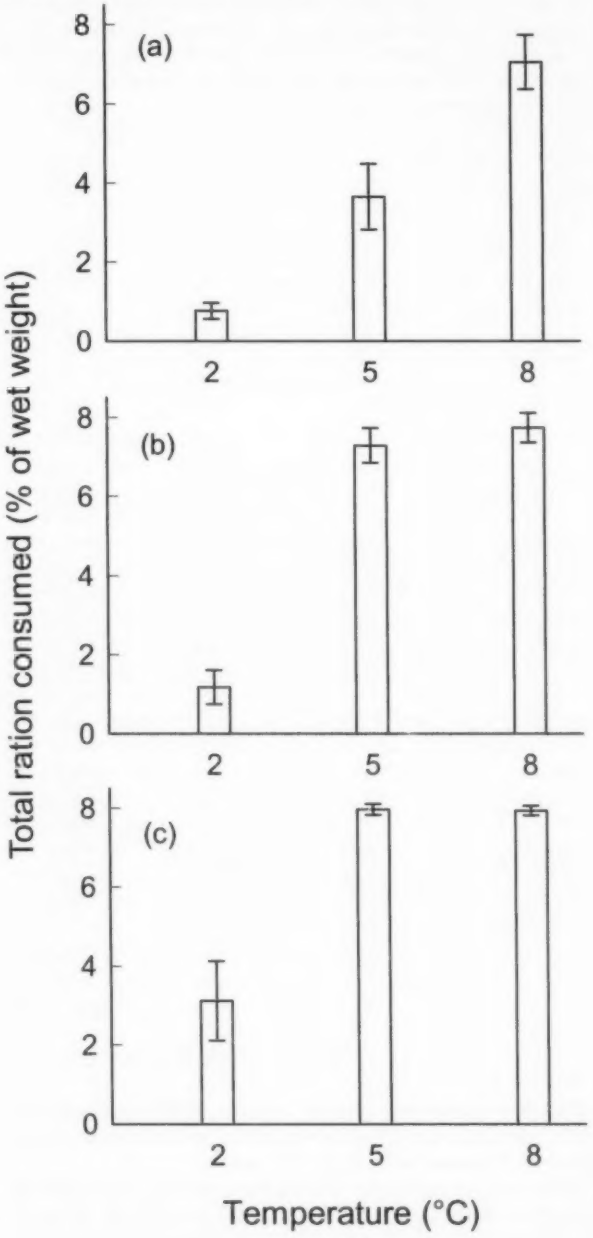
Bait attacks and consumption

The proportions of baits attacked and consumed by sablefish were dependent upon both temperature and feeding history (Table 2). One hundred percent of the squid presented to sablefish at 8 °C were consumed. The same was true for fish at 5 °C, except that after 1 day of food deprivation, 12% of the squid were left untouched and 21% were never consumed. Fish at 2 °C had much lower attack and consumption rates; 29–67% of the squid were not consumed. All of the baits offered to fish acclimated to 8 °C water temperature were consumed upon the first location and inspection, regardless of food deprivation time (Table 3). In 5 °C water, sablefish ultimately consumed most of the baits, but the baits were frequently inspected or handled and rejected multiple times before eventual consumption. All of the baits offered in 5 °C water were inspected, bitten, or consumed, but the number of handlings and rejections increased with decreasing food deprivation. Fish in 2 °C water did not always respond to baits (Table 3), and the majority of baits were inspected or handled multiple times before a complete bite and consumption was made. An individual bait was often encountered two to five times before it was touched by the sablefish in the coldest treatment, and the number of rejected baits increased with decreasing food deprivation.

The effect of temperature on the median number of squid consumed (considering only the three baits presented initially) was significant for fish deprived of food for 1 and 3 days but not for fish deprived for 6 days (Table 1). The effect of food deprivation was not significant in any of the three temperature treatments, even at 2 °C (Table 1), because of large variation among individual tanks.

When the total ration of squid consumed by sablefish in the 1-h feeding period was considered in the analysis (Fig. 2), there was a significant effect of temperature for each of the food deprivation treatments (Table 1). The ration consumed at 2 °C was always less than that consumed at the higher temperatures. The total rations consumed by fish held at 5 and 8 °C were different only at 1 day of food deprivation, when fish at 8 °C ate the most squid. Although the total ration consumed generally increased with increasing food deprivation, the effect of deprivation was significant only for sablefish in the 5 °C treatment (Table 1).

Fig. 2. Ration of squid (% of fish wet weight) consumed by sablefish in three different temperatures and at three levels of food deprivation over a 1-h feeding trial: (*a*) 1 day, (*b*) 3 days, and (*c*) 6 days. Values are mean ± SE for each combination of temperature and food deprivation (n = 8).



Attack and handling times

Temperature had a large effect on the time required to make the first attack on the baits, whereas the effect of food

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Table 3. Summary of responses to baits by sablefish held in three different temperatures and with three periods of food deprivation.

Temperature (°C)	Food deprivation (days)	No. of baits consumed with no previous inspections or handling	No. of baits consumed after previous inspections or handling	No. of baits inspected or handled but rejected	No. of baits never inspected or handled
2	6	13	4	4	3
2	3	5	6	11	2
2	1	2	6	9	7
5	6	22	2	0	0
5	3	21	3	0	0
5	1	13	6	5	0
8	6	24	0	0	0
8	3	24	0	0	0
8	1	24	0	0	0

Note: Twenty-four total baits were offered in each of the experimental conditions (see Materials and methods for details).

deprivation was small (Fig. 3). Fish at 8 and 5 °C and with 3 and 6 days of food deprivation took just 4–8 s, on average, to make a first bite on each of the three squid offered in a tank. Recently fed (1 day) fish at 5 °C took 35 s to make first bites, and fish at 2 °C took 1.2–40 min to bite. Time to first attack decreased with food deprivation (Fig. 3). The effect of temperature was significant for all deprivation levels, whereas the effect of food deprivation on time to first attack was not significant (Table 1) because of wide variation among the tanks, particularly at 2 °C.

Many of the squid baits attacked were not consumed (Table 2). However, the total time taken to consume baits followed a pattern nearly identical to that of time to first attack (Fig. 3). The time to complete bite decreased significantly with increasing water temperature, regardless of feeding history (Table 1). These times also decreased with food deprivation and were particularly apparent at 2 °C (median values ranged 11–49 min) and 5 °C (0.2–2.4 min), but the differences were significant only for fish at 5 °C (Table 1) because of either large variation or small changes in the medians observed (just 6–9 s at 8 °C).

The primary variable influencing squid handling time was temperature (Fig. 4) (Table 1), with times typically an order of magnitude longer for fish held at 2 °C compared with those at 8 °C. Fish at 8 °C often required essentially no handling time, drawing their prey into a complete bite with one inhalation, whereas fish in the lower temperatures often made several tentative bites and rejections of the squid before consumption. The effects of feeding history on handling time were not significant for any of the three temperatures tested (Table 1), although mean handling times of fish at 2 °C decreased from 22 to 11 s with increasing food deprivation.

Discussion

The effective area surveyed with baited fishing gear depends upon the active space of the bait, fish encounters with the scent plume, the proportion of fish responding to the scent, and the proportion locating, attacking, and being captured on the bait (Eggers et al. 1982). Løkkeborg et al. (1995) showed that hunger level in sablefish has a major impact on the active space of a bait because olfactory thresholds for response decrease with increasing food deprivation. In our experiments, food deprivation period had several significant effects on responsiveness to bait-related cues and baits. The indices of post-cue activity increased with hunger in sablefish at 5 and 8 °C but not at 2 °C, suggesting that swimming speeds and the general intensity of search behavior are likely to be greatest in hungry fish and warm water. However, the proportional increase in activity before and after olfactory cues were introduced did not differ substantially with food deprivation. This appears to be related to the fact that both metrics of activity are related to food deprivation, particularly at the higher temperatures. Food deprivation had a large effect on responsiveness to actual baits. Numbers of baits taken, the total ration consumed, time to attack baits, and bait handling times all decreased with hunger, particularly in fish held at 2 and 5 °C. Relatively low effects of food deprivation period on fish held in 8 °C undoubtedly resulted from the fact that these fish digested their meals quickly (He and Wurtsbaugh 1993) and were at a high hunger level after 24 h of deprivation.

The impact of temperature on complex behavioral responses (e.g., activity level, attack rates, time to attack) was greater than the effect of food deprivation in most cases. First, without olfactory stimulation, indices of activity in sablefish were 10–75% higher at 8 °C than at 2 °C, and fish at 2 °C were frequently observed resting on the bottom. Others have shown that temperature affects activity and swimming speeds in fishes (He 1993; Bradford and Higgins 2001; Hurst and Conover 2001), including juvenile sablefish (Sogard and Olla 2001), and direct effects of temperature on other behavior patterns are likely. Activity indices in scent-stimulated fish were 55–91% higher at 8 °C than at 2 °C, with the greatest differences in fish deprived of food for 6 days, as would be expected.

Variation in attack rates and times could also have a major impact on the catchability of sablefish. Although all three baits presented initially at 8 °C were attacked and consumed, the numbers consumed were lower at 2 and 5 °C, depending upon level of food deprivation. The effect of food deprivation on consumption time was significant only at 5 °C, but the attack and consumption times varied by several orders of magnitude over the temperatures tested. At low temperature, baits were frequently located but simply passed over or tentative bites were made, and handling times increased by 6–14 times.

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Fig. 3. Time to attack (open bars) and consume (hatched bars) squid baits by sablefish in three different temperatures and at three levels of food deprivation: (*a*) 1 day, (*b*) 3 days, and (*c*) 6 days. Values are medians with 25% and 75% quartiles for eight trials in each of the treatment combinations.

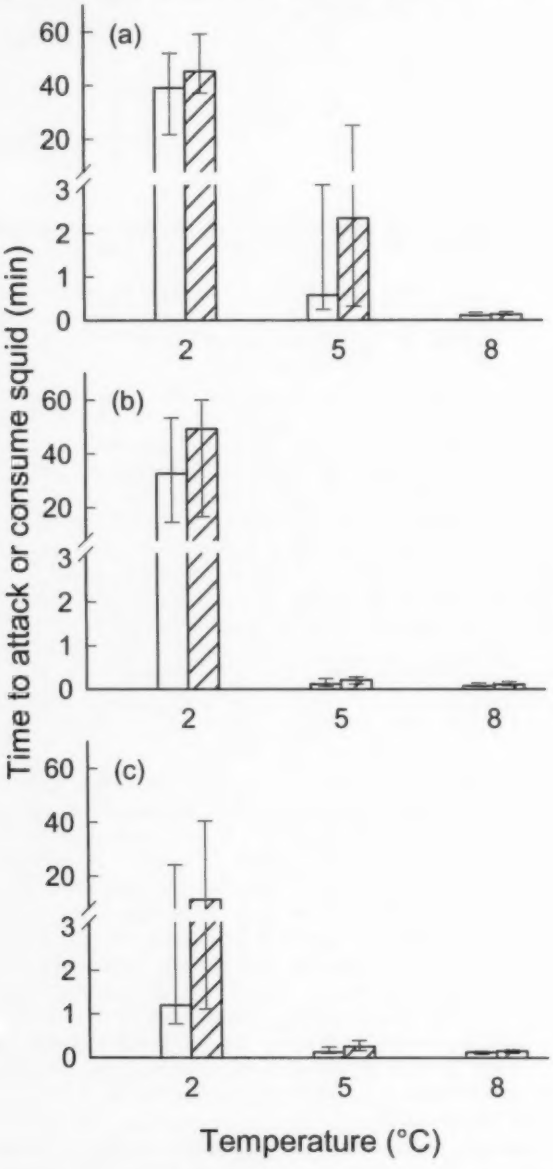
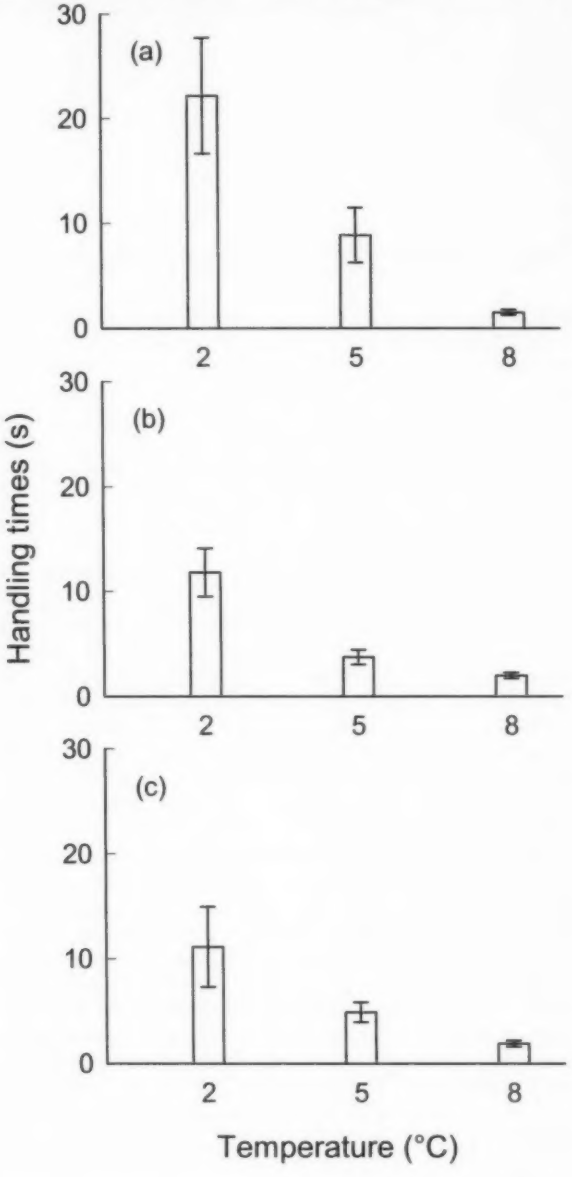


Fig. 4. Handling time for squid baits consumed by sablefish in three different temperatures and at three levels of food deprivation: (*a*) 1 day, (*b*) 3 days, and (*c*) 6 days. Values are mean ± SE for each combination of temperature and food deprivation (n = 8).



The effects of temperature on the behavioral responses observed can result from both direct and indirect mechanisms. As previously discussed, temperature effects on swimming behavior are well known and there may be other direct effects on feeding behavior. However, it is also likely that feeding motivation and attack frequencies were mediated indirectly through metabolic rates. Digestion and metabolism are strongly influenced by temperature in ectotherms (He and Wurtsbaugh 1993), and the links between metabolic processes, feeding, and growth are well known (Colgan 1986; Croy and Hughes 1991; Angilletta et al. 2002). In laboratory experiments, Sogard and Olla (2001) found that activity levels, consumption rates, and growth rates in juvenile sablefish all increased with temperature. In our study, food consumption by sablefish at 2 °C remained low (3.1% of wet weight) even after 6 days of food deprivation, and consumption was a linear function of temperature with 1 day of deprivation. Given a feeding-intense strategy that results in extraordinarily high growth rates in sablefish

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(Sogard and Olla 2002), it is not surprising that feeding motivation corresponded directly to temperature and feeding history.

A logical extension of the experiments discussed here would be to standardize hunger level in different temperature conditions. This would require knowledge of the relationships between temperature, gut fullness, hunger, and other physiological processes. However, data provided in this study provide insights into digestion rates and the relationships to feeding motivation. Sablefish held in 2 °C and deprived of food for 6 days consumed 39% of a full ration. A similar ration (45%) was consumed by fish held in 5 °C and deprived for just 1 day. Consequently, digestion was approximately six times faster in 5 °C than in 2 °C fish, following patterns observed in other fishes (He and Wurtsbaugh 1993). Other performance metrics including general activity, attack rates, attack times, and handling times were nearly equal in these two groups of fish. This suggests that activity and feeding performance are, in fact, directly related to stomach fullness, which is temperature mediated. Given that an 87% ration was consumed by sablefish in 8 °C after just 1 day versus 8% in 2 °C fish, digestion in 8 °C fish occurs ~10 times faster than in 2 °C fish. Thus, metabolically mediated feeding motivation in sablefish varies by an order of magnitude over their normal range of temperature distribution.

Sigler (1993) noted that catch rates (and stock assessments) made from the numbers of sablefish caught on longline gear could be affected by factors other than population density, including bait competition, current velocity, hooked fish attracting other fish, and fish depletion. Later, he mentioned the possible effect of temperature on sablefish catch rates using longline gear (Sigler 2000). It is difficult to interpret laboratory results directly in terms of field impacts, and our intent was not to develop correction coefficients for stock assessment models. However, laboratory investigations with sablefish (Løkkeborg et al. 1995; this study) show that Sigler's concerns about the potential effects of environmental conditions were correct.

Prey availability and temperature are two of the most variable parameters in nature over scales of both time (e.g., tide, season, and year) and space (bathymetric and geographic). Feeding is dependent upon prey density, in part, and the effects of feeding history on sablefish responsiveness to chemical cues associated with bait can result in several orders of magnitude variation in active space (Løkkeborg et al. 1995). In addition, our experiments show significant effects of both recent feeding and low temperature on sablefish including reduced sensitivity to olfactory cues, lower swim speed, increased rejection of baits upon inspection, lower attack rates, much increased time to attack, and lower total consumption. Reduced sensitivity to olfactory cues and lower swim speeds subsequent to bait detection means that the probability of sablefish in cold water encountering a bait will be reduced. In contrast, fish in warm water will cover greater areas searching for the source of a food scent and locate baits faster than in cold water. Because scent levels in the field would probably be lower than those presented in this experiment and because olfactory thresholds decline with increasing hunger, it is likely that temperature-related differences in fish responsiveness is even more pronounced in the ocean. Low bite frequency, incomplete bites, and extended attack and handling times observed in cold water combined with recent feeding will greatly reduce the catchability of sablefish, compounding the effects of low swim speeds and bait detection to further reduce the effective area of baited gear. Moreover, cautious or tentative attacks made in cold conditions will further reduce the number of fish hooked. The complexity of the relationship between temperature, feeding behavior, and activity precludes making precise estimates for the impact of temperature on the effective area of fishing gear at this time. However, the potential differences are large, and stock abundance could be grossly underestimated in cold-water conditions or where natural prey are abundant.

It is now clear that the internal (physiological) state of the target species along with its sensory capabilities and external (environmental) conditions can have major impacts on bait detection, locomotion, and feeding motivation (Løkkeborg et al. 1995; Stoner 2003; this study). Consequently, we make the following recommendations related to stock assessments conducted with baited fishing gear. (*i*) Environmental data should be taken concurrent with survey operations. Given the ease of recording and the obvious, large effect of temperature, this variable should have high priority. (*ii*) Corrections for temperature-related variability in fish catchability and gear effective area need to be developed and applied to stock assessments. Our data on feeding motivation indicate that correction factors will need to span at least one order of magnitude for the natural temperature range of sablefish. (*iii*) Comparisons of catch rates should be made between baited gear and bait-independent approaches in a variety of conditions to assist in evaluating important effects of environmental variables. (*iv*) Increased experimental effort is needed to understand the relationship between environmental variables, catch rates, and stock assessments for economically significant species.

Acknowledgements

We thank Susan Sogard for collecting sablefish and Michele Ottmar, Mara Spencer, Paul Iseri, and Scott Haines for maintenance of the fish and assistance in running experiments. Paul Iseri assisted with analysis of videotapes. Richard Titgen provided help with video systems, lighting, and graphics for the manuscript. Michael Davis, Thomas Hurst, and anonymous reviewers provided helpful criticisms on the manuscript.

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Assessing population sustainability and response to fishing in terms of aggregation structure for greenlip abalone (*Haliotis laevigata*) fishery management

Natalie A. Dowling, Stephen J. Hall, and Richard McGarvey

Abstract: The greenlip abalone (*Haliotis laevigata*) population in Waterloo Bay, South Australia, has undergone collapse and fishery closure twice since 1978. A rich data set, including survey measures of degree of spatial aggregation, has been gathered over that time and provides a unique opportunity to identify factors accounting for persistence or collapse, an issue that is of significance to abalone fisheries worldwide. Statistical analyses of fishery and survey data were undertaken to infer functional relationships between catch, effort, recruitment, adult density, and extent of aggregation. Catch rates were hyperstable, an observation consistent with the targeting of large aggregations. Statistical analysis of recruitment showed a significant year effect, implying an environmental signal, and suggested that aggregation size impacts fertilization success. Aggregation size grew under closure, suggesting an impact of fishing on this demographic feature. Aggregative behaviour appears to be critical for subpopulation sustainability. Fishery collapse may be triggered by depletion of larger abalone aggregations by heavy fishing, resulting in declines in fertilized egg production. When heavy fishing coincides with unfavourable environmental conditions, recruitment may be insufficient to sustain the subpopulation. If aggregation is similarly critical for other subpopulations, management strategies could be adapted according to the extent of aggregation in each subpopulation.

Résumé : La population de l'ormeau *Haliotis laevigata* de la baie de Waterloo en Australie du Sud a subi un effondrement et, à deux reprises depuis 1978, la pêche commerciale en a été interdite. Pendant cette période, cependant, se sont accumulées d'importantes banques de données, en particulier des mesures d'inventaire du degré de contagion spatiale; c'est là une occasion unique d'identifier les facteurs qui expliquent la persistance ou l'effondrement de la population, une question d'importance pour les pêches commerciales d'ormeaux partout dans le monde. Des analyses statistiques des données de pêche et d'inventaire ont permis de mettre en évidence des relations fonctionnelles entre les captures, les efforts de pêche, le recrutement, la densité des adultes et le degré de contagion. Les taux de captures sont hyperstables, ce qui s'explique par le ciblage des grands regroupements. Les analyses statistiques du recrutement révèlent un effet significatif de l'année, ce qui laisse croire qu'il existe un signal de l'environnement et que la taille des regroupements affecte le succès de la fertilisation. La taille des regroupements augmente lorsque la pêche est interdite, indiquant que la pêche affecte cette caractéristique démographique. Le comportement de regroupement semble jouer un rôle essentiel dans le maintien des sous-populations. L'effondrement du stock semble être déclenché par l'élimination des grands rassemblements à cause d'une pêche intensive qui entraîne un déclin dans la production d'oeufs fécondés. Lorsque la pêche intensive coïncide avec des conditions environnementales défavorables, le recrutement peut ne pas suffire à maintenir la sous-population. Si les rassemblements sont aussi essentiels chez d'autres sous-populations, les stratégies de gestions peuvent être adaptées selon les niveaux de contagion de chacune des sous-populations.

[Traduit par la Rédaction]

Introduction

The greenlip abalone (*Haliotis laevigata*) is extensively harvested in South Australia for export to Asia. The stock consists of approximately 300 subpopulations, three of which (Waterloo Bay, Backstairs Passage, and Avoid Bay) have experienced population collapse (Shepherd and Rodda 2000). A subpopulation is defined as a group of abalone occurring in clusters on patches of loosely connected habitat that together form a local population whose spatial dimensions are of the

Received 16 October 2002. Accepted 29 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 31 March 2004.
J17144

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 doi: 10.1139/F03-165 © 2004 NRC Canada

scale over which the habitat is continuous (usually tens to hundreds of metres). Local populations are then grouped into metapopulations whose spatial dimension is of the scale of larval dispersal and mixing (Shepherd and Brown 1993). To date, the causes of collapse in these subpopulations have not been formally investigated. However, McShane (1995), Shepherd and Partington (1995), and Shepherd and Brown (1993) suggested that the situation is more complex than one of simple overfishing and that a dynamic understanding of fishing intensity, factors affecting recruitment, and the importance of aggregations (Gorfine et al. 1998) is required before the factors responsible for collapses may begin to be identified.

As in most fisheries, abalone management strategies are generally implemented on a broad spatial scale. Specifically, the *H. laevigata* stock for the state of South Australia is divided into three management units, each on the order of hundreds of kilometres of coastline: the southern, central, and western zones (Keesing and Baker 1998). However, collapses have occurred at the subpopulation level (e.g., reefs or bays). The persistence under exploitation of subpopulations managed identically but with different egg production and recruitment characteristics has been highly variable (Shepherd and Baker 1998). This suggests that management regulations should be tailored to individual subpopulations, notably those for which indicators suggest declining abundance (Prince and Shepherd 1992; Shepherd and Brown 1993; McShane 1995).

In this study, we investigated the greenlip subpopulation in Waterloo Bay (Elliston, South Australia), which has experienced two collapses (1979 and 1987). Subsequent to each collapse, the bay was closed to fishing (from 1982 to 1986 and from 1995 to the present), with the exception of two controlled "fish-downs" in 1998 and 1999. Annual research surveys have been conducted in the bay since 1978 (Shepherd and Partington 1995), and a spatially resolved catch–effort database has been maintained since 1967. Of particular value are a semiregular time series of survey measures of the degree of abalone aggregation. Thus, there exists for this subpopulation a detailed data history spanning two fishery collapses and closures. The population is thought to be largely or entirely self-propagating (Shepherd and Brown 1993; Shepherd and Partington 1995).

Our objective was to infer the functional relationships between catch, effort, recruitment, adult density, and level of aggregation. These data are examined using generalized linear modelling to find the predictor variables accounting for annual variation in catch and recruitment and thus provide insight into the factors that are most important for abalone population sustainability. Temporal trends in egg-to-recruit survival and reevaluations of Shepherd and Partington's (1995) stock–recruitment relationship and temporal aggregation data are considered in the context of the results of the statistical models. Our goal was to identify key factors accounting for population persistence or collapse in Waterloo Bay and thus formulate a basis for improved management and fishery models.

Methods

Data

The fishery-dependent and -independent variables used in the analyses are defined in Table 1. Data were available from Waterloo Bay from 1975 to 1999. During this time, the following events are noteworthy: (*i*) the bay was closed to fishing between 1982 and 1986 and from 1995 to 1998 and (*ii*) in 1998 and 1999, the bay was opened for 2 weeks to limited quota fishing within a size slot of 125–145 mm total length (the longest section of the shell).

Fishery-independent surveys were undertaken immediately before and after the size-slot fishing in 1998 and 1999. In 1998, surveys consisted of random swims and trials of a line transect method. Details of each method can be found in Appendix A. The prefishing (April) data were obtained from 57 random swims and 11 line transects (2089 individual abalone counted), and the postfishing (May) data were obtained from 46 random swims and eight line transects (1217 individuals counted). In 1999, April data were obtained from 65 random swims and 74 line transects (4797 individuals counted) and May data from 68 random swims and 81 line transects (4829 individuals counted). Aggregation data were combined across both types of surveys. It should be noted that the catch and effort data from these two years were not used in the statistical catch models or analyses because the values are affected by the imposition of a quota.

Data on aggregation patterns were obtained from surveys of aggregation size distributions from 1982, 1984, 1986, and 1988 (published as fig. 7 in Shepherd and Partington 1995) and from 1998 and 1999 (before and after fish-down). Data from 1982 to 1988 were combined across the three geographical relief categories ("low", "medium", and "high") used by Shepherd and Partington (1995). Aggregations binned by Shepherd and Partington (1995) in the aggregation size class ">26" were conservatively assigned the aggregation size range of 26–30 individuals. In the 1998 and 1999 surveys, the size of each aggregation encountered was explicitly recorded. Following Shepherd and Partington (1995), the size of an aggregation was defined as the number of abalone greater than 120 mm total length less than 1 m from the nearest neighbour. A distance of 1 m was chosen because modal nearest-neighbour distances are 20–30 cm (Shepherd and Partington 1995) but also because individuals greater than 1 m apart show a dramatic decline in fertilization success with increasing distance from their nearest neighbour (Babcock and Keesing 1999). For the line transect surveys, only aggregations whose size could be fully viewed from the line were recorded. For larger aggregations that extended beyond the transect edge, divers left the transect line to count the individuals.

To summarize changes in aggregation patterns over time, the mean aggregation size was then calculated for each year as follows:

$$(1) \qquad \bar{i} = \sum_{i=1}^{n} (iP_i)$$

where i is aggregation size and P_i is the proportion of individuals found in aggregation size i.

Exploratory statistical analysis

To investigate the critical factors affecting the population sustainability, three response variables were investigated: catch, recruitment, and aggregation structure.

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Table 1. Primary data and secondary data for Waterloo Bay from 1976–1997.

Time series	Symbol	Source	Years available	Description
Primary data				
Catch	*C*	Monthly commercial catch logs: South Australian Reasearch and Development Institute (SARDI) records	1975–1999	Kilograms meat weight harvested by commercial divers. Meat weight assumed to be one third of the total weight
Fishing effort	*E*	Monthly commercial catch logs: SARDI records	1975–1999	Total hours spent underwater by commercial divers
Recruitment	*R*	Research dive surveys conducted by S.A. Shepherd	1976–1990, 1994, 1996–1999	Numbers per 100 m^2 for the 2-year-old age class ("cohort") determined using modal separation of length–frequency distributions (Shepherd and Partington 1995)
Mean adult stock density	*D*	Research dive surveys conducted by S.A. Shepherd	1976–1990, 1994, 1996–1999	Numbers per square metre for individuals ≥4 years of age determined using modal separation of length–frequency distributions (Shepherd and Partington 1995)
Aggregation frequency distributions	Not applicable	Shepherd and Partington 1995; research dive surveys conducted by S.A. Shepherd and N.A. Dowling	1982, 1984, 1986, 1988, 1998, 1999	Frequency distributions of individuals in aggregation size categories. Aggregations defined as the number of individuals >120 mm total length found <1 m from their nearest neighbour (Shepherd and Partington 1995)
Secondary data				
Index of fertile gamete production	IFGP	Shepherd and Partington 1995	1976–1990	An index of biomass weighted for the degree of aggregation calculated as the product of the aggregated spawning biomass (a linear function of adult density) and the fertilization success factor F, where $F = \sum_{i=1}^{n} P_i E_i$, P_i is the proportion of individuals, and E_i is the proportion of eggs fertilized in aggregations of the ith size) (Shepherd and Partington 1995)
Survival of an average egg to age 2	*R*/IFGP	Derived	1976–1990	Recruitment (density of 2-year-old age class) divided by the IFGP giving an index for the survival of an average egg to age 2
Fishery index	FISH	Monthly commercial catch logs: SARDI records	1975–1999	Binary index indicating whether the fishery was open in a given year. This index removed any effect of the fishery status from the year factor in statistical models. Any resulting effect attributed to year was thus independent of that resulting from the status of the fishery

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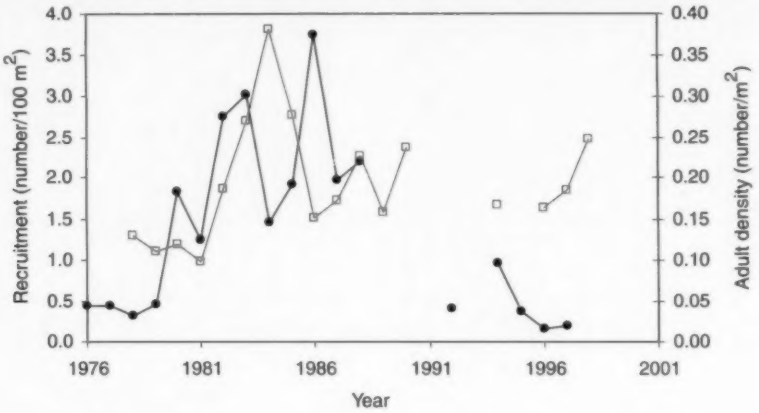
Fig. 1. Surveyed estimates of adult density (squares and shaded line) and recruitment (2-year-olds, lagged by 2 years to correspond to year of spawning) (circles and solid line) versus year obtained using the timed random swim technique.



Combinations of annual catch, effort, catch-per-unit-effort (CPUE), and adult biomass were plotted and their regression coefficients compared in an attempt to identify systematic bivariate relationships and potentially important predictor variables for catch. Auto- and cross-correlation were used to test for periodic trends in time series and time lags in correlations between recruitment (of 2-year-olds) and adult biomass, recruitment and the index of fertile gamete production (IFGP) (see Table 1), and survival to age 2 and adult biomass. The cross-correlation function, $r_{xy}(k)$, measures the degree of correlation between variables x_t and y_{t+k}, where k is the lag number (Chatfield 1975).

Recruitment values were lagged by 2 years to associate the recruitment density, defined as the density of 2-year-old abalone (Table 1), with the year of spawning. A generalized Deriso equation gave a better fit to the data, in terms of both least squares and overall shape, than the Ricker stock–recruitment relationship presented by Shepherd and Partington (1995). The equation, modified to include an x-intercept, as described by Chen et al. (2002), is of the form

$$(2) \qquad R = \alpha(\mathrm{IFGP} + c)[1 - \beta(\mathrm{IFGP} + c)/\Gamma]^{\Gamma}$$

where R is recruitment, IFGP is the index of fertile gamete production (Table 1), and α, β, Γ, and c are fitted parameters.

Catch and recruitment were more formally investigated using generalized linear models. The advantage of such models is that they allow explanatory variables to be collectively examined to determine the relative contribution of each to the variation in the response. Each yields single linear coefficients associated with each predictor. Residual and quantile–quantile plots were used to assess model fit. As such, recruitment was modelled assuming a Gamma error distribution and a log link function, whereas catch and effort were square root transformed and the square root catch was modelled assuming a Gaussian error distribution and an identity link function to relate the mean of the behavioural parameter to its linear predictors (Crawley 1993).

The minimum adequate model for each response variable (catch and recruitment) was determined by sequential deletion of terms from a full model. Significant changes in deviance associated with the deletion or change of an explanatory variable from the model, as determined by F test, implied that the explanatory variable had a significant influence on catch or recruitment. Model fits were assessed using residual, fitted value and quantile–quantile plots.

The full catch and recruitment linear models tested were

$$(3) \qquad \sqrt{C} = \alpha_1\sqrt{E} + \alpha_2 D + \alpha_3(\mathrm{YR}) + \varepsilon$$

$$(4) \qquad R = \beta_1 D + \beta_2(\mathrm{IFGP}) + \beta_3(\mathrm{YR}) + \beta_4(\mathrm{FISH}) + \varepsilon$$

where C and R are the response variables catch and recruitment, E, D, and IFGP are the numeric explanatory variables effort, adult density, and index of fertile gamete production, YR and FISH are the explanatory variables year and fishery status index (open or closed), treated as factors, α_i and β_i are single linear coefficients, and ε is an error term.

To investigate aggregation structure, mean aggregation size was plotted against year, and cluster analysis was performed on the frequency distributions for 1982–1988 and 1998–1999. This indicated the degree of relatedness between distributions from different years and, for 1998 and 1999, those observed before and after fish-down events. For the 1998 and 1999 data, the χ^2 test was employed to determine whether the frequency distributions before and after fishing in each year differed significantly.

Results

Recruitment analyses

Peaks in recruitment lagged those in adult density by 2 years (Fig. 1), and the cross-correlation function for adult density versus recruitment was maximized at a lag number of two ($r_{xy}(2) = 0.724$). That is, recruitment was most positively (and significantly ($r_{\mathrm{df}=8,\alpha=0.05} = 0.632$, $P < 0.05$)) correlated with adult density 2 years subsequently. Recalling that recruitment equates to the density of 2-year-old abalone, shifted back 2 years to correspond to the year of spawning, the density of 2-year-old abalone was strongly positively correlated with the density of adults in the same year.

Similarly, the cross-correlation function was maximized at a lag number of 2 for both combinations of IFGP versus recruitment and adult density versus survival to age 2 (R/IFGP)

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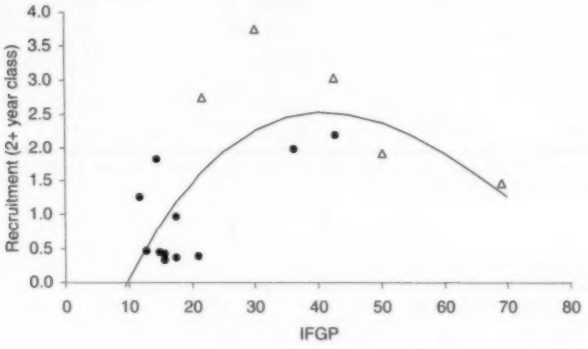
Fig. 2. Generalized Deriso stock–recruitment equation (curved line) fitted to 16 data points representing annual estimates of recruitment and IFGP (index of fertile gamete production, an index of biomass weighted for the degree of aggregation). Circles, surveyed recruitment during years of fishing; triangles, surveyed recruitment during closure years. Adapted from Shepherd and Partington (1995).



($r_{xy}(2) = 0.789$ and $r_{xy}(2) = 0.801$, respectively). Both cross-correlation coefficients were statistically significant ($r_{df=8,\alpha=0.05} = 0.632$, $P < 0.05$). That is, the density of 2-year-old abalone was positively correlated with the index of biomass weighted by the degree of aggregation (IFGP) (Table 1), and survival to age 2 was positively correlated with adult density in the year in which the recruits turn 2 years old.

Cross-correlations for recruitment versus adult density and recruitment versus IFGP did not show a strongly positive cross-correlation function at any lag number (for lag number = 0, $r_{xy}(0) = 0.242$ ($r_{df=10,\alpha=0.05} = 0.576$, $P > 0.05$) and $r_{xy}(0) = 0.288$ ($r_{df=10,\alpha=0.05} = 0.576$, $P > 0.05$), respectively). Thus, recruitment success was not positively correlated with the adult abundance in the year of spawning.

The cross-correlation function for survival to age 2 (*R*/IFGP) versus adult density was negative for all lag numbers but was highest in magnitude at lag number 0 ($r_{xy}(0) = -0.433$). Although this correlation coefficient is not statistically significant ($r_{df=10,\alpha=0.05} = 0.576$, $P > 0.05$), it suggests that a high adult density resulted in a low survival rate to age 2 for abalone spawned in the same year.

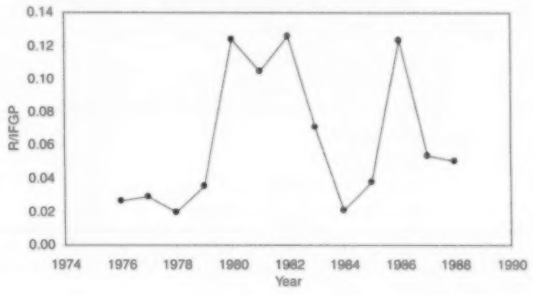
The relationship between stock, expressed as IFGP (the index of biomass weighted by the degree of aggregation), and recruitment was best described by the following Deriso equation, which was fitted to 16 data points (Fig. 2):

$$(5) \qquad R = 0.176(\mathrm{IFGP} - 9.696) \times [1 - 0.020(\mathrm{IFGP} - 9.696)/1.665]^{1.665}$$

Maximum recruitment occurs at IFGP = 42, which corresponds to an adult density of ~0.22 adults·m^{-2} (significant linear regression between adult density and IFGP ($r^2 = 0.92$)). Three of the four data points to the right of this maximum (including the highest two IFGP values) are from the years in which the bay was closed to fishing.

A time series plot of survival to age 2 (calculated as *R*/IFGP) (Fig. 3) exhibited an oscillatory trend with peaks in 1980–1982 and 1986. Indeed, autocorrelation analysis yielded a maximum, although not statistically significant, autocorrelation coefficient at a lag of $k = 6$ years for *R*/IFGP ($r_6 = 0.224$, $r_{0.05(2),6} = 0.707$, $P > 0.05$).

Fig. 3. Time series plot for an index of the survival of an average egg to age 2 calculated as *R*/IFGP (recruitment divided by the index of fertile gamete production). The plot indicates an oscillatory trend with peaks in 1980–1982 and 1986.



Recruitment patterns were most adequately described by a linear model of IFGP (adult biomass weighted for aggregation) and year:

$$(6) \qquad R = -19.05(\mathrm{IFGP}) - 0.3446(\mathrm{YR}) - 0.0096(\mathrm{IFGP} \times \mathrm{YR}) + 683.83$$

where IFGP × YR is the interaction between IFGP and YR (Table 2).

This model reduced the null deviance by 72.8% for a loss of 3 degrees of freedom compared with the null model (Table 2). There was a significant interaction between year and IFGP (Table 3). Both IFGP and adult density, *D*, were used as indices of biomass in the models, but IFGP was a significantly better predictor in terms of residual deviance (Table 3), albeit at the cost of 2 degrees of freedom (Table 2). Importantly, the effect of fishing was treated as a separate factor, and so the significant year effect was not due to the status of the fishery.

Catch analyses

Catch showed a strong positive-linear relationship with effort ($r^2 = 0.98$) (Fig. 4*a*) that was highly significant (regression ANOVA: $F = 1462.91$, df = 1, 27, $P = 0$) but no significant relationship to adult density ($r^2 = 0.37$) (Fig. 4*b*) (regression ANOVA: $F = 4.15$, df = 1, 7, $P = 0.08$). This implies that catch is independent of abundance but is a strong linear function of effort. Further, adult density showed no significant relationship with respect to CPUE ($r^2 = 0.20$) (Fig. 4*c*) (regression ANOVA: $F = 1.76$, df = 1, 7, $P = 0.23$). This suggests that CPUE is not proportional to greenlip abalone abundance in Waterloo Bay.

Linear models also indicated that effort accounted for the majority of variation in catch. There was also a significant interaction effect between effort and year, whereby effort decreased over time. The minimum adequate model was

$$(7) \qquad \sqrt{C} = 3.898\sqrt{E} + 17.301D - 5.293\sqrt{E} \times D - 4.776$$

where $E \times D$ is the interaction between effort and adult density. This model reduced the null deviance by 98.3% (see Table 4 for analyses of deviance).

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Table 2. Analysis of deviance tables for linear models predicting recruitment.

Number	Model	Null deviance	Null df	Residual deviance	Residual df
1	$R \sim$ IFGP + CALYR + D + FISH	7.0630	12	2.3910	8
2	$R \sim$ IFGP + CALYR + FISH	7.0630	12	3.1708	9
3	$R \sim$ IFGP + FISH	7.0630	12	6.2369	10
4	$R \sim$ CALYR + FISH	12.5763	16	12.3192	14
5	$R \sim$ IFGP + CALYR	7.0630	12	4.2629	10
6	$R \sim$ IFGP + CALYR + IFGP × CALYR[a]	7.0630	12	1.9227	9
7	$R \sim$ IFGP	7.0630	12	6.3289	11
8	$R \sim$ CALYR	12.5763	16	12.5200	15
9	$R \sim D$ + CALYR	10.1899	14	9.4843	12
10	R ~ D + CALYR + FISH	10.1899	14	8.9077	11

Note: The null degrees of freedom vary because of variations in the number of available data points for the response variables included in each model. ~, modelled as a function of; CALYR, calendar year; IFGP × CALYR, interaction term for IFGP and CALYR.
[a]Minimum adequate model.

Table 3. Results from ANOVAs comparing the recruitment linear models.

Models compared	Variable tested	Change in deviance	F	$P(F)$
2 vs. 3	YR	3.0661	8.5063	0.0171275*
2 vs. 4	IFGP	9.1484	5.0762	0.017334*
2 vs. 5	FISH	1.0921	3.0300	0.1157253 ns
5 vs. 6	IFGP and YR interaction term	2.3403	10.8510	0.0093175**
5 vs. 9	D as compared with IFGP	5.2213	6.2680	0.0172038*
4 vs. 10	D	3.4114	1.6466	0.2353892 ns

Note: *, Significant at the 5% level; **, significant at 1% level; ns, not significant at the 5% level.

Consistent with Figs. 1–3, catch was not related to adult density and year but was highly linearly dependent on effort. The interaction effect between adult density and effort was weaker when the 1986 data point was excluded (Table 5). In 1986, the fishery was reopened after the 4-year closure and experienced a greater increase in effort relative to the corresponding increase in adult density that had taken place, resulting in the two variables becoming aliased.

Aggregation data

After the closure of the fishery in 1982, individuals showed a progressive trend towards larger (≥20) aggregation sizes (Figs. 5*a*–5*c*). After the reopening of the fishery in 1986, fewer individuals were found in larger aggregations by 1988 (Fig. 5*d*). However, this reduction of larger aggregation sizes did not approach the 1982 distribution observed before closure, possibly because of the newly imposed larger size limit of 145 mm total length as opposed to 130 mm (Shepherd and Partington 1995). Mean cluster size, a parameter sensitive to the intensity of aggregation (Shepherd and Partington 1995), showed a similar trend between 1982 and 1988 (Fig. 6); its magnitude increased from approximately 5 to 11 after the fishery closure and declined to below 9 in 1988 (recall that the maximum aggregation size had been conservatively set at 30 individuals).

Cluster analysis of the 1982–1988 distributions yielded results consistent with Figs. 5 and 6. A Bray–Curtis similarity dendrogram (Fig. 7) showed that the distributions for 1984 and 1986 were more closely related to one another than to the 1988 distribution and that the 1982 distribution showed the least degree of relatedness to any of the other distributions.

Unlike the 1982–1988 data, for which aggregations over the size of five had been binned, the specific sizes of each aggregation were recorded in 1998 and 1999. The April 1998 aggregation frequency distribution (Fig. 8*a*) reflects the population aggregation structure after 3.5 years of closure to fishing. The maximum aggregation size surveyed was 190 individuals, and 30% of surveyed abalone occurred in aggregations ≥20. Three aggregations larger than 80 individuals were recorded. After the 1998 fish-down, where licensees were permitted a 50-kg (meat weight) quota, only one aggregation >80 was observed during surveys (Fig. 8*a*), and the proportion of individuals in aggregations of 20 or more individuals had dropped to 18%.

After the 1998 fish-down, the population was unfished until April 1999. The survey immediately before the commencement of the 1999 fish-down showed the population collecting into larger aggregation sizes (Fig. 8*b*), with 25% of surveyed individuals in aggregations of 20 or more. Four aggregations of more than 80 individuals were recorded; however, the proportion of individuals in aggregations of more than 80 did not approach that of April 1998 (Fig. 8*a*). Licensees each removed 150 kg (meat weight), and after fishing, the population again contracted towards smaller aggregation sizes (Fig. 8*b*), with only 15% of individuals found in aggregations ≥20. Only one aggregation >80 was observed. In both 1998 and 1999, the proportion of individuals in aggregations of two to four increased by 24% and 29% respectively.

Mean aggregation size showed a decrease from 37 to 19 after the 1998 fish-down, an increase to 22 over the next 11 months, and a decline to 14 after the 1999 fish-down (Fig. 9). Cluster analysis of the 1998 and 1999 distributions indicated that between-year

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Fig. 4. Scatterplots of (*a*) financial year catch versus effort (underwater), (*b*) financial year catch versus surveyed adult density, and (*c*) financial year CPUE versus adult density, each with fitted regression lines.

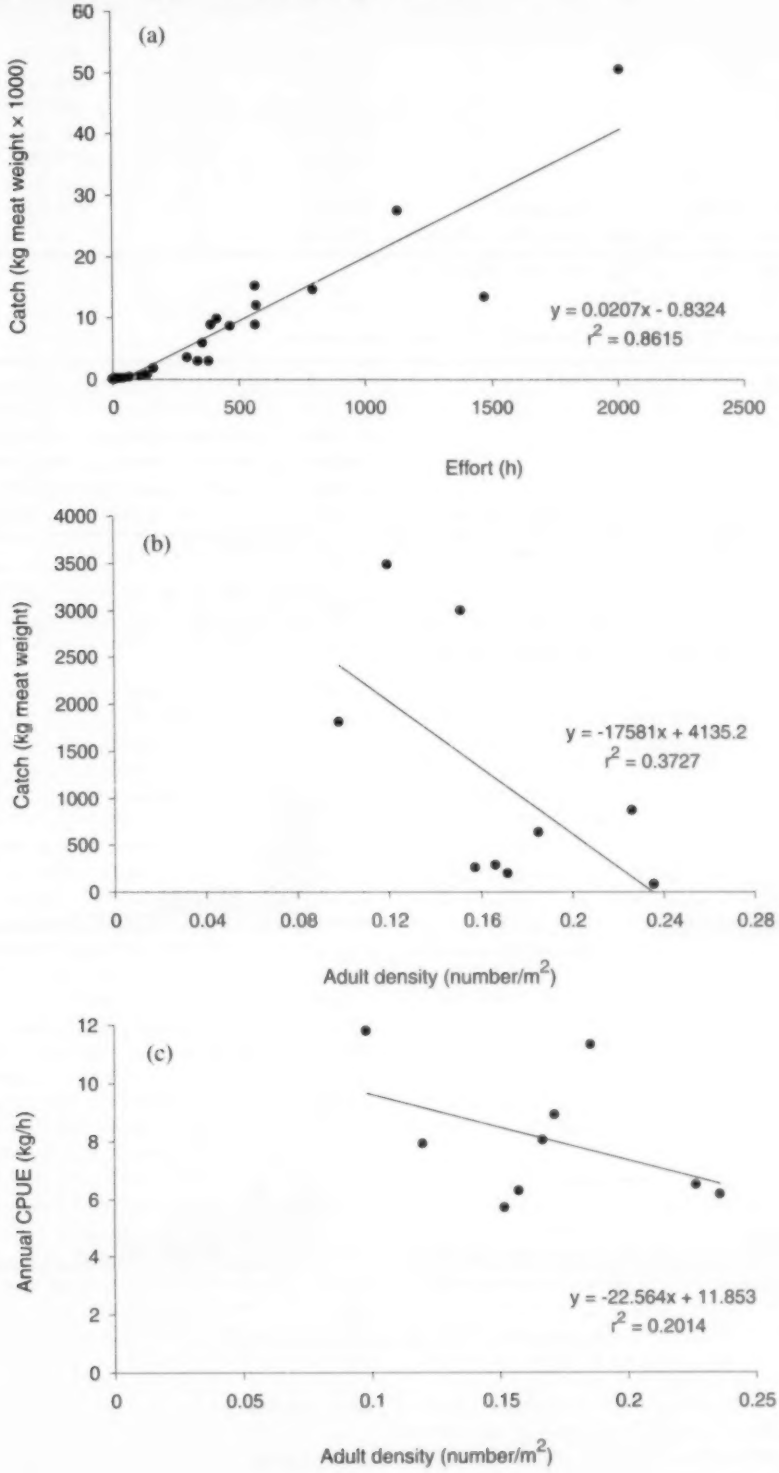

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Table 4. Analysis of deviance tables for linear models predicting catch.

Number	Model	Null deviance	Null df	Residual deviance	Residual df
1	$C \sim E + D$ + CALYR	6883.085	14	160.005	11
2	$C \sim E$ + CALYR	6893.589	18	185.704	16
3	$C \sim D$ + CALYR	6883.085	14	3248.432	12
4	$C \sim E + D$	6883.085	14	160.009	12
5	$C \sim E$	6893.589	18	186.328	17
6	$C \sim D$	6883.085	14	4719.080	13
7	$C \sim E + D + E \times D$[a]	6883.085	14	118.719	11
8	$C \sim E + D$ with 1986 data point excluded	5301.836	13	156.220	11
9	$C \sim E + D + E \times D$ with 1986 data point excluded	5301.836	13	118.073	10

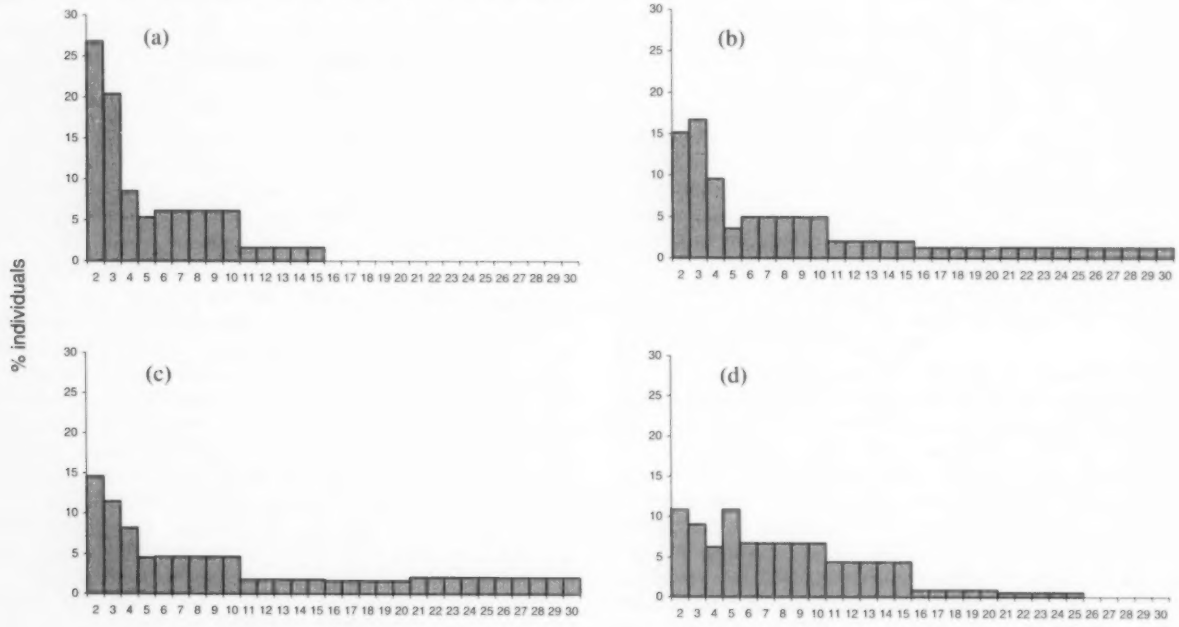
Note: ~ modelled as a function of; $E \times D$, interaction term for E and D.
[a]Minimum adequate model.

Table 5. Results from ANOVAs comparing the catch linear models.

Models compared	Variable tested	Change in deviance	F	$P(F)$
1 vs. 2	D	25.6988	0.3533	0.8697 ns
1 vs. 3	E	3088.4270	212.3225	1.54586×10^{-8}**
1 vs. 4	CALYR	0.0040	0.0003	0.9871 ns
4 vs. 7	$D \times E$	41.2898	3.8257	0.0763 ns
8 vs. 9	$D \times E$ excluding 1986 data	38.1471	3.2308	0.1025 ns

Note: *, Significant at the 5% level; **, significant at the 1% level; ns, not significant at the 5% level.

Fig. 5. Frequency distributions of the proportion of individuals in each aggregation size for (*a*) 1982, (*b*) 1984, (*c*) 1986, and (*d*) 1988 (adapted from Shepherd and Partington 1995). Aggregations greater then 5 were binned by 5 up to the "plus" class of ≥26. The final category was conservatively truncated at an aggregation size of 30.



variability was greater than the within-year variability induced by fishing (Fig. 10). However, χ^2 analyses indicated a significant difference between the pre- and post-fishing distributions for both the 1998 data ($\chi^2_{df=15,\alpha=0.05} = 172.8$, $P = 0$) and 1999 data ($\chi^2_{df=20,\alpha=0.05} = 648.6$, $P = 0$).

Discussion

Recruitment

The fitted Deriso stock–recruitment equation, together with the negative correlation between survival to age 2 and adult

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Fig. 6. Mean aggregation size versus year for 1982–1988 data. Error bars are ±1 SE.

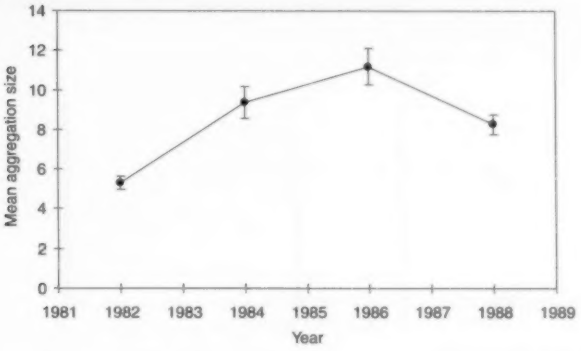
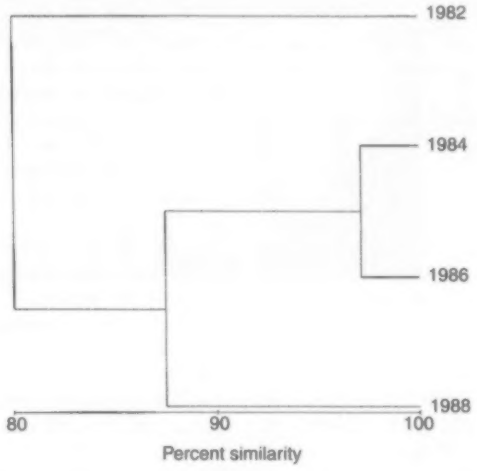


Fig. 7. Bray–Curtis similarity dendrogram from cluster analysis illustrating the degree of relatedness for aggregation size–frequency distributions for 1982–1988.



density, shows that density dependence occurs. Shepherd and Partington (1995) suggested that the IFGP corresponding to the recruitment maximum on the stock–recruitment curve is a threshold value above which density dependence takes place and below which the subpopulation is vulnerable to overexploitation. That three of the data points in the "density-dependent" regime of the curve (i.e., to the right of the fitted recruitment maximum) correspond to the years of fishery closure supports this notion. The likely mechanism responsible for density dependence is limitation in appropriately sized crevices to shelter the juveniles, which are then vulnerable to predation.

Attempts to derive stock–recruitment relationships for other South Australian greenlip abalone populations such as Avoid Bay and Cape Jervis resulted in an apparently random scatter of stock–recruitment data (Shepherd and Rodda 2000). The ability to define an underlying stock–recruitment relationship for fisheries that typically have high fecundity and high larval dispersal has been disputed (Underwood and Fairweather 1989; Koslow 1992) because small changes in prerecruit natural mortality lead to large changes in survivorship (Koslow 1992). As the Waterloo Bay subpopulation is isolated with no external larval sources (Shepherd and Brown 1993), it is reasonable to consider stock–recruitment dynamics within the subpopulation. Indeed, Prince et al. (1988) showed a strong relationship between local population breeding stock density and recruitment (albeit on a scale of metres) in blacklip abalone (*Haliotis rubra*).

Although a threshold IFGP for overexploitation may be a reasonable concept, it is not explicit with respect to the mechanisms responsible for recruitment failure, since IFGP is a variable constructed from three variables: adult stock density, fertilized egg production, and degree of aggregation. Using linear modelling, both IFGP and a year effect were shown to significantly affect recruitment. As the status of the fishery had no significant effect on recruitment, the year effect was attributed to an environmental signal. The latter may also have been responsible for the oscillating time series for survival of an average egg to age 2 (*R*/IFGP). The nature of this signal has not been identified. However, the CPUE for sand crabs in Coffin Bay, Eyre Peninsula, also shows a 6-year periodic oscillation such as that found for survival to age in Waterloo Bay greenlip abalone (Jones 1995; Jones and Deakin 1997). Additionally, Venus Bay prawns and west coast rock lobster CPUEs follow the same 6-year oscillation as the sand crab CPUE (G.K. Jones, SARDI Aquatic Sciences, P.O. Box 120, Henley Beach, South Australia 5022, Australia, personal communication). This may suggest a large-scale environmental signal affecting invertebrate fisheries on the west coast of South Australia.

Linear modelling showed that IFGP (an index of biomass weighted by the degree of aggregation) was a better predictor of recruitment than adult density. This suggests that aggregation size has a significant impact on recruitment, most likely in terms of fertilization success. Abalone are broadcast spawners, and it has been shown experimentally (Babcock and Keesing 1999) that fertilization success is a negative-exponential function of near-neighbour distance for greenlip abalone. As larger aggregations have a lowered average near-neighbour distance and a higher local density, their probability of fertilization success for broadcast gametes increases. Group size (4 individuals versus 16 individuals) and degree of aggregation (0.25 individual·m^{-2} versus 4 individuals·m^{-2}) were shown to significantly affect fertilization success in sea urchins (Levitan et al. 1992). Indeed, it is on this assumption that Shepherd and Partington (1995) calculated the IFGP parameter. The proportion of eggs E_i fertilized in each aggregation i was derived from the results of Levitan (1991) and Levitan et al. (1992) for sea urchins.

Validity of recruitment

Cross-correlation analyses showed that the density of 2-year-old abalone was strongly positively correlated with the adult abundance (adult density or IFGP) in the same year. That is, if adult density is high in a given year's survey, so is the density of 2-year-olds. Survival to age 2, calculated as *R*/IFGP, was also strongly positively correlated with the adult density surveyed in the same year as the recruitment density.

This suggests that recruitment estimates may be biased by overall abundance. The small size of 2-year-old abalone (40–80 mm) makes them difficult to detect in surveys, and as such, recruitment estimates are based on very small observed numbers. For example, of the 2612 abalone measured in May 1999, only 26 fell into the length category for 2-year-

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Fig. 8. Frequency distributions of the proportion of individuals in each aggregation size for April (prefishing, solid bars) and May (postfishing, open bars) in (*a*) 1998 and (*b*) 1999. Note that the maximum aggregation size is 190 for 1998 and 120 for 1999.

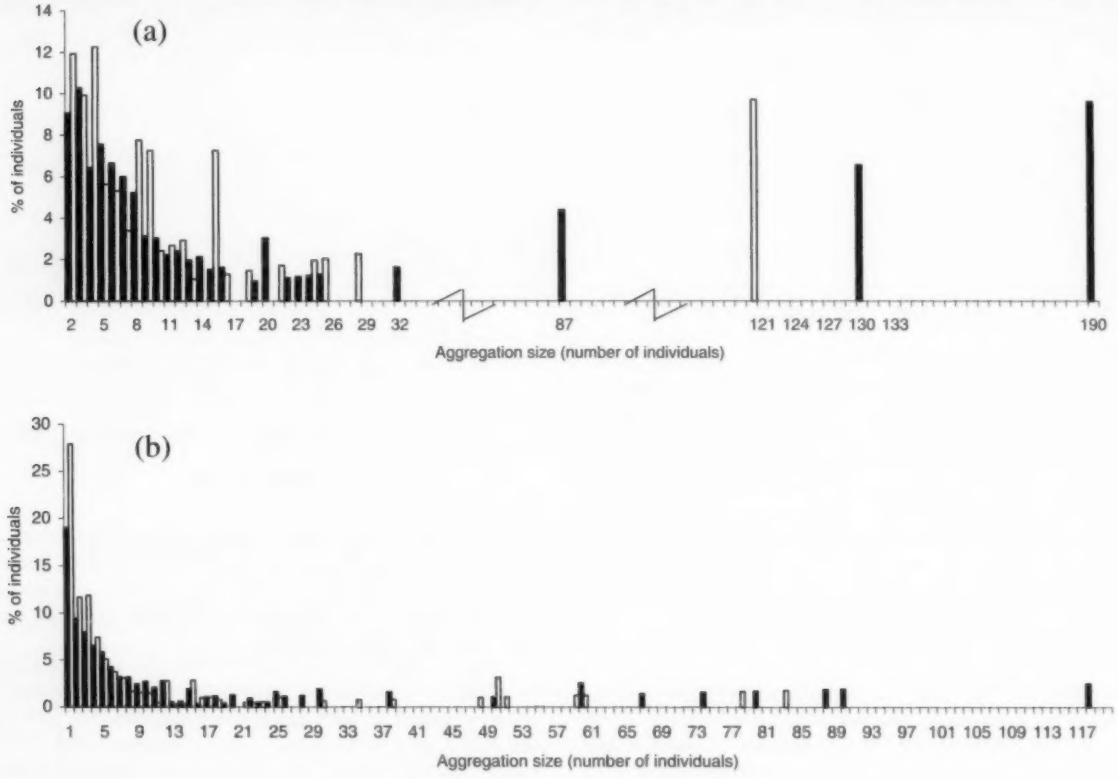
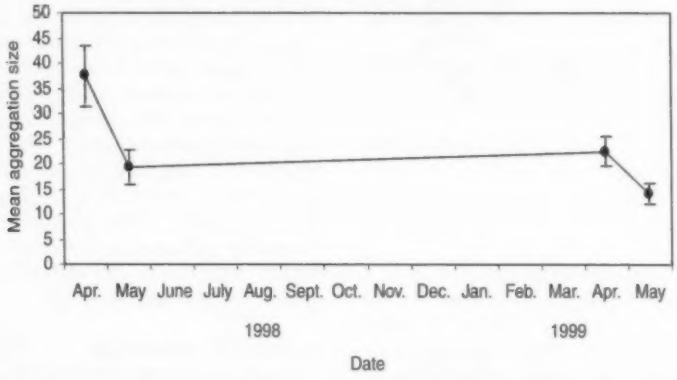


Fig. 9. Mean aggregation size versus time for 1998 and 1999 data. Error bars are ±1 SE.



old individuals. It may be that when overall abalone abundance is high, the observer spends more time looking closely at the bottom and thereby is more likely to notice smaller abalone. Whatever the case, the cross-correlation results indicate that recruitment densities should be used with caution.

Catch

Catch in Waterloo Bay was linearly proportional to effort and independent of density and year, whereas CPUE also showed no relationship with adult density. The bivariate relationships between catch or CPUE and adult density were not positive-linear; indeed, both relationships showed negative associations. This supports Prince's (1992) conclusion that catch or CPUE should not be used as an index of abundance for abalone. It also implies that the traditional catch equation (Schaefer 1954)

$$C = qEB \quad (8)$$

where C is catch, q is the catchability coefficient, E is effort, and B is biomass, does not apply to this fishery because annual

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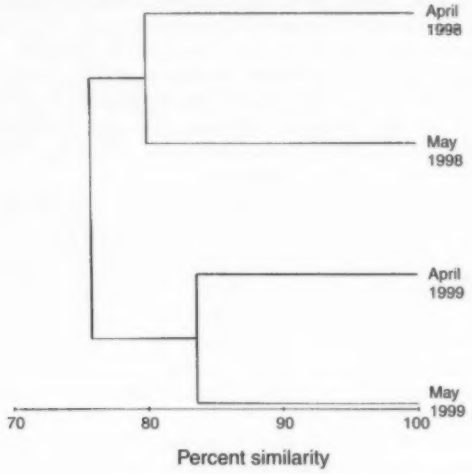
Fig. 10. Bray–Curtis similarity dendrogram from cluster analysis illustrating the degree of relatedness for aggregation size–frequency distributions for April and May in 1998 and 1999.



catch was shown to be solely a function of effort (confounded by year). Biomass is more likely to influence catch in terms of a discrete threshold level below which fishers give up searching. However, this "cutoff" situation has not been observed for Waterloo Bay.

These results are consistent with the concept that abalone actively aggregate (Shepherd 1986; Prince 1992; Gorfine et al. 1998) and abalone divers target the aggregations. The implication is that the abalone subpopulation behaves similarly to a pelagic fishery in that the prey (abalone) continually reaggregate and the fishers hunt the aggregations (Hilborn and Walters 1992). If divers spend little time randomly searching for abalone, checking the condition of known "abalone beds" by looking at the state of an abalone bed's aggregations before deciding whether to dive in that location, catch tends to remain proportional to the time spent diving (Prince 1989; Prince et al. 1998). As such, catch is a linear function of effort and is not sensitive to the depletion of the surrounding biomass that replenishes the aggregations. Potentially, the ultimate situation under continued effort is one of hyperdepletion and fishery collapse (Hilborn and Walters 1992).

Aggregation

The correlation of trends in aggregation with the status of the fishery, whereby larger aggregations are formed in the absence of fishing and are reduced to smaller aggregations when fishing takes place, suggests that fishing has a significant effect on aggregation frequency distributions. The increase in the proportion of individuals in larger clusters after fishery closure is consistent with the implication of the results for catch that fishing targets and depletes large aggregations. It must be emphasized that the above analyses do not show conclusively that commercial abalone divers target large aggregations. This issue is addressed in Dowling et al. (2004). However, when the above results are considered in the context of that of Babcock and Keesing (1999) that fertilization success is a function of near-neighbour distance, it may be concluded that the depletion of larger aggregations has serious implications for reproductive success.

Hypotheses for population sustainability

The analyses conducted suggest two hypotheses. The first is that cyclic environmental factors impact the Waterloo Bay subpopulation to reduce the recruitment success of an average egg on a 6-year period. At this stage, the environmental factor has not been conclusively identified. The second hypothesis is that aggregative behaviour has a critical role with respect to subpopulation sustainability. Although this has been suggested indirectly by Prince (1992), McShane (1995), and Shepherd and Partington (1995), these results provide the first statistical evidence to support this hypothesis. It appears that exploitation targets aggregations, which are believed to have the greatest contribution to reproductive success (Babcock and Keesing 1999), so that the most significant contributors to fertilized egg production are those that are the most vulnerable to exploitation. Aggregation level appears to drive the population dynamics to a greater extent than does absolute biomass. Therefore, rather than proposing an IFGP level below which the subpopulation is vulnerable to overfishing (Shepherd and Partington 1995), it may be preferable to consider a critical aggregation frequency for adequate fertilization success and to define the degree of vulnerability to fishing in terms of aggregation structure. A more simple management strategy may be to designate areas known to contain large aggregations as reserves, although enforcement would be difficult.

It is tentatively hypothesized that fishery collapse in the Waterloo Bay greenlip abalone subpopulation is due to overfishing resulting in the depletion of larger aggregation sizes, which in turn implies a decline in fertilized egg production. When this is combined with unfavourable environmental conditions, recruitment may be insufficient to sustain the subpopulation.

The issues of hyperstability and recruitment overfishing, resulting in the rejection of CPUE as a valid index of abundance, have implications for spatially heterogeneous fisheries in general. How fish are distributed and how fishers allocate their fishing effort in space are essential ingredients in understanding how a fishery develops and the relationship between catch rate and abundance (Hilborn and Walters 1987). In this context, the findings are applicable to schooling pelagic stocks where CPUE is a poor index of abundance, such that schooling leads to a strong depensatory effect (Clark 1974). The purse-seine fishery, where floating attraction devices are used to aggregate tuna species, is an example of such a fishery, as is the northern cod fishery. Incorporating aggregation structure in a model of the latter explained how cod vulnerability to fishing could increase with declining stock biomass (Hutchings 1996).

Waterloo Bay is perceived by fishers and fishery managers to be a "unique" subpopulation that is not representative of abalone population dynamics and responses to fishing because of its history of heavy fishing and closure. Although management strategies should account for subpopulation variability, it is important to ensure that the factors affecting Waterloo Bay subpopulation sustainability are reflective of the population dynamics for the species. To validate these conclusions in a broader context, if aggregation can be shown

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to be a critical factor for population sustainability for other subpopulations with different histories of sustainability, then there may be a basis for generalization across subpopulations. If this is the case, management strategies may be adapted given the extent of aggregation in each subpopulation.

Acknowledgments

The authors wish to thank the assistance of Dr. Scoresby Shepherd who generously supplied data and much advice during the development of this paper. Dr. Jeremy Prince and two anonymous reviewers provided helpful criticism on the manuscript. This work was undertaken as part of a Ph.D. study funded by an Australian postgraduate award.

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Appendix A. Description of random swim and line transect methods

In both years, an experienced five- or six-member research team conducted dive surveys in Waterloo Bay in the week immediately preceding and in the week after the opening period. The spatial grid from previous years was used to subdivide the bay into 20 survey blocks (Fig. A1). The ma-

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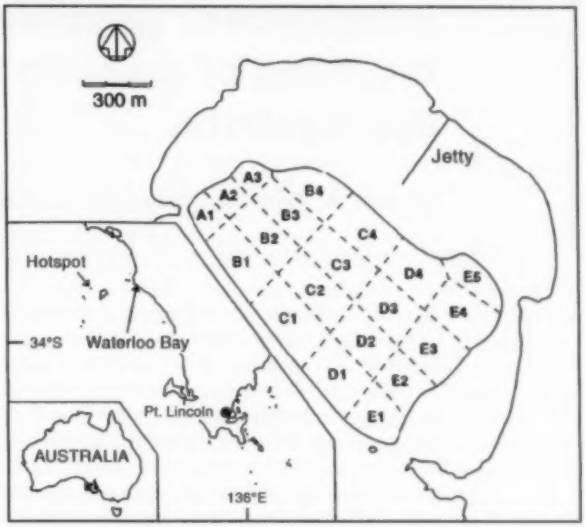
jority of these were surveyed in each year, but swell and visibility restricted access to some blocks. Four days of diving was required to complete each set of surveys. Diving was not necessarily conducted on consecutive days, as inclement weather sometimes prohibited surveying. However, a complete survey did not take longer than 7 days to complete.

In 1998 and 1999, the blocks were surveyed using the timed random swim technique (Shepherd 1985). Divers swam in a random direction for 10 min, during which time they measured in situ the length of all greenlip abalone encountered, with the exception of aggregations greater than four individuals, in which case they measured four abalone. This was the existing survey protocol designed to maximize the area surveyed by limiting the time spent measuring. The size of each aggregation encountered was also recorded. Following Shepherd and Partington (1995), the size of an aggregation was defined as the number of abalone greater than 120 mm standard length less than 1 m from the nearest neighbour. A distance of 1 m was chosen because modal nearest-neighbour distances are 20–30 cm (Shepherd and Partington 1995) but also as a functional definition based on reproductive success; individuals greater than 1 m apart show a dramatic decline in fertilization success with increasing distance from their nearest neighbour (Babcock and Keesing 1999).

A line transect technique was also used to survey the greenlip population in 1998 and 1999. The line transect technique is a form of distance sampling that has been used extensively for terrestrial ecological surveys (Buckland et al. 1993). It has also been used for censuses of commercial reef fishes (Kulbicki 1998) but was trialed for abalone for the first time during the 1998 survey periods and incorporated into the survey protocol in 1999 to estimate abundance.

The line transect technique involved swimming in a straight line for 50 m using a reel with a line, marked at 50-m intervals, attached to a stable object on the bottom. The number of abalone in each aggregation as seen from the line was recorded, together with an approximation of the perpendicular distance of the centre of the aggregation to the line to the nearest half-metre. As it is an assumption of the technique that every individual located directly about the line was detected, divers examined the area under the line thoroughly, moving aside algae and checking under rock overhangs. Having completed a 50-m transect, the diver would swim laterally for a distance of approximately 20 m and conduct a replicate 50-m transect by reeling in the line while swimming along this second radius back to the anchor point. This procedure would then be repeated in the opposite direction so that four replicate 50-m transects would ideally be obtained in a single dive. The locations for transects were randomly determined, were not stratified, and were not revisited identically on subsequent surveys.

Fig. A1. Map of Waterloo Bay illustrating the survey block subdivisions.



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Simulations of random fishing behaviour as an independent validation for the effect of active targeting of greenlip abalone (*Haliotis laevigata*) aggregations

Natalie A. Dowling, Stephen J. Hall, and Richard McGarvey

Abstract: Although active targeting of abalone aggregations is documented for various species, its impact on large aggregations is poorly understood. As large aggregations make the greatest contribution to reproductive success, yet are vulnerable to exploitation, it is important to understand how targeted fishing impacts aggregation structure. If observed postfishing patterns are equally likely to have occurred in response to more random, nontargeted fishing, then changes in aggregation patterns cannot be directly attributed to aggregation-based targeting behaviour. The effect of targeted fishing on greenlip abalone (*Haliotis laevigata*) aggregations was verified by simulating three different levels of "random" fishing behaviour to generate postfishing aggregation frequency distributions. Comparison of the output with postfishing survey distributions suggested that observed aggregation patterns could not have resulted from random search behaviour. The aggregation survey data can therefore be used as a valid basis on which to quantify both fishing behaviour in terms of aggregation-specific catch patterns and the response of aggregations to fishing.

Résumé : Bien que le ciblage actif des regroupements d'ormeaux ait été étudié chez plusieurs espèces, on en connaît mal l'impact sur les grands regroupements. Puisque les grands regroupements contribuent majoritairement au succès de la reproduction et qu'ils sont vulnérables à l'exploitation, il est important de comprendre comment la pêche ciblée affecte la structure des regroupements. Si les patterns observés après la pêche peuvent vraisemblablement s'être formés en réaction à une pêche plus aléatoire et non ciblée, les changements dans les patterns de contagion ne peuvent s'expliquer directement par un comportement de ciblage basé sur la contagion. Nous avons vérifié les effets de la pêche ciblée sur les regroupements de l'ormeau *Haliotis laevigata* en simulant trois niveaux différents de pêche « aléatoire » dans le but de générer des distributions de fréquence des regroupements après la pêche. La comparaison des résultats des simulations et des répartitions inventoriées après la pêche montre que les patterns de contagion observés ne peuvent être générés par un comportement de recherche aléatoire. Les données d'inventaire sur la contagion peuvent donc servir de base valide pour quantifier, d'une part, le comportement de pêche en ce qui a trait aux patterns de capture spécifiques aux regroupements et, d'autre part, la réaction des regroupements à la pêche.

[Traduit par la Rédaction]

Introduction

Greenlip abalone (*Haliotis laevigata*) show a strong tendency to form and maintain aggregations, which renders them vulnerable to fishing (Shepherd 1984; Shepherd and Partington 1995; Dowling et al. 2004). In a movement experiment, individual greenlip abalone set in a regular pattern 1 m apart almost all moved into aggregations within 3 days (Shepherd 1984). It is broadly accepted that commercial abalone divers target large aggregations of abalone (Prince 1992; McShane 1998; Shepherd and Rodda 2000). Divers search visually with the primary objective of maximizing catch rates (Keesing and Baker 1998; Prince and Hilborn 1998; Prince et al. 1998). Assuming that divers have good information about the population distribution, or can rapidly determine this as they fish by "skimming" the area (Prince 1989), exploitation should be initially centred about the largest aggregations and gradually shift to smaller aggregations until a threshold is reached at which fishing is no longer profitable (Prince and Hilborn 1998). Divers spend little time randomly searching for abalone (Prince et al. 1998). Rather, they check the condition of known "abalone beds"

Received 16 October 2002. Accepted 29 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 31 March 2004.
J17145

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 doi: 10.1139/F03-164 © 2004 NRC Canada

by looking at the state of an abalone bed's best aggregations before deciding whether or not to dive in that location.

Analyses for greenlip abalone in Waterloo Bay, South Australia, support the notion that divers target greenlip aggregations. Larger aggregations formed in the absence of fishing, which were eliminated when fishing recommenced, and catch was independent of overall abundance and linearly proportional to effort (Dowling et al. 2004). This is consistent with active targeting of aggregations. If divers spend little time randomly searching for abalone, checking the condition of known abalone beds by looking at the state of an abalone bed's aggregations before deciding whether to dive in that location, catch tends to remain proportional to the time spent diving (Prince 1989; Prince et al. 1998). Indeed, before a fishery closure in 1982, Waterloo Bay catch rates remained high despite the declining abalone abundance (Shepherd and Baker 1998). This was because adult abalone continually migrated to reefs of high relief where they were targeted by fishers (Shepherd and Baker 1998). Information from 1998 and 1999 diver interviews and questionnaires also implied that large aggregations are targeted, in that divers fish to a threshold catch rate or search for "good bottom" in terms of abalone habitat before fishing an area.

Although the active targeting of aggregations is well documented across a number of abalone species, the impact of this fishing behaviour on subpopulations is not well understood. McShane (1995) showed a high frequency of small aggregations in heavily fished populations and a relatively high frequency of large patches in an unfished population. However, fish-down experiments conducted on greenlip abalone in Waterloo Bay in 1998 and 1999 are the only abalone surveys to directly assess the impact of fishing on the aggregation structure of a subpopulation.

Since the targeted, large aggregations make the greatest contribution to reproductive success (Babcock and Keesing 1999), it is critical to verify how targeted fishing impacts aggregation structure and to ensure that observed postfishing aggregation distributions reflect targeting behaviour unambiguously. If observed aggregation patterns are equally likely to have occurred in response to random fishing, then changes in aggregation patterns cannot be directly attributed to aggregation-based targeting behaviour. If aggregation frequency distributions are to be used to quantitatively describe targeted fishing behaviour (e.g., determining an aggregation-specific catchability) and the impact of targeted fishing on aggregations, it must first be confirmed that the postfishing aggregation distributions could not have been observed had a randomly fishing strategy been used.

In this study, we investigated the impact of targeted fishing on aggregation structure. We aimed to verify statistically the effect of targeted fishing on abalone aggregation structure by confirming, using a series of Monte Carlo simulations, that aggregation patterns observed after fishing events are directly attributable to targeted fishing on large aggregations.

Methods

Data

After its closure to fishing in late 1995, Waterloo Bay was opened in 1998 and 1999 for 2 weeks to limited quota fishing within a size slot of 125–145 mm total length (the longest section of the shell). Results from independent surveys undertaken immediately before and after the size-slot fishing in each year were used in the Monte Carlo simulations to test the null hypothesis that aggregation frequency distributions observed immediately after fish-downs could have occurred as a result of employing a purely random fishing strategy. In 1998, surveys consisted of random swims and trials of a line transect method. Locations for the random swims and line transects were chosen randomly within each survey block. Full details of each survey method can be found in Dowling et al. (2004). In 1998, the prefishing (April) data were obtained from 57 random swims and 11 line transects (2089 individual abalone counted, aggregation size recorded for 1987 individuals), and the postfishing (May) data were obtained from 46 random swims and eight line transects (1217 individuals counted). In 1999, April data were obtained from 65 random swims and 74 line transects (4797 individuals counted, 2148 measured to obtain length–frequency data) and May data from 68 random swims and 81 line transects (4829 individuals counted). The data were obtained by pooling the results of replicate random swim and line transect surveys made in most of the 20 block subdivisions in Waterloo Bay.

Following Shepherd and Partington (1995), the size of an aggregation was defined as the number of abalone >120 mm total length <1 m from the nearest neighbour. A distance of 1 m was chosen because modal nearest-neighbour distances are 20–30 cm (Shepherd and Partington 1995) but also as a functional definition based on reproductive success; individuals >1 m apart show a dramatic decline in fertilization success with increasing distance from their nearest neighbour (Babcock and Keesing 1999). For the line transect surveys, only aggregations whose size could be fully viewed from the line were recorded. For larger aggregations that extended beyond the transect edge, divers left the transect line to count the individuals.

Surveyed prefishing aggregation distributions were used as input to the simulations, and the output of simulated fishing was compared with the observed postfishing aggregation distributions. The distributions consisted of the proportion of individuals in each unique aggregation size from 2 to 190 in 1998 and from 1 to 120 in 1999 (the frequency of single abalone was not recorded in 1998).

Simulated fishing strategies

Results from surveys made immediately before and after fish-down experiments in 1998 and 1999 were used to test whether observed postfishing aggregation patterns differed significantly from either targeted or random fishing strategies. This was achieved via a series of Monte Carlo simulations that used the surveyed prefishing aggregation distributions as input. The output of simulated fishing was compared with the observed postfishing aggregation distributions. The distributions consisted of the proportion of individuals in each unique aggregation size from 2 to 190 in 1998 and from 1 to 120 in 1999.

As the extent of random fishing is a matter of degree, three alternative fishing strategies were considered, each having a different degree of "randomness". The first most closely approached targeted fishing on large aggregations. Each individual abalone was given an equal probability of being

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"encountered by a diver", and it was assumed that once an individual had been detected, so was the aggregation in which it occurred, and all legal-sized abalone found in that aggregation were removed. By assigning an equal detection probability to all individuals, larger aggregations indirectly had a higher probability of being "fished" because of their higher relative proportion of individuals.

The second strategy also assigned an equal probability of removal to all individuals, but other members of the same aggregation were not taken at the same time. As with the first strategy, individuals from larger aggregations had a higher probability of being removed because of their larger relative proportion. However, the probability of large aggregations being removed was lower than for the first strategy, since aggregation structure was disregarded.

The third strategy assigned an equal "encounter" probability to each aggregation. That is, each aggregation size had an equal chance of being "detected by a diver", and so there was no weighting towards larger aggregations. Thus, this strategy was the most random in terms of its degree of targeting of larger aggregations. As with the first strategy, it was assumed that all legal-sized abalone would be detected and removed.

Simulation structure and analysis of output

For each simulation, the 1998 and 1999 aggregation distributions surveyed were assumed to be representative of the subpopulation. For each year (1998 and 1999), the prefishing aggregation distributions, made in April immediately before the opening of the bay to fishing, were used as the simulation input. The sample sizes for these distributions were 1987 individuals in 1998 and 4797 in 1999. To provide a larger simulated sample size, the number of aggregated individuals surveyed in 1998 was multiplied by 2 to give 3974 rather than 1987 individuals (thus also doubling the number of aggregations).

Reported catch was scaled relative to the number of aggregated individuals surveyed because the simulated catch was removed from the surveyed individuals, which were assumed to be representative of the whole population. The proportion of the population removed was calculated using estimates of catch-by-numbers (Appendix A) and of overall subpopulation size from surveys (obtained by multiplying density of abalone by habitat area). Estimates of abalone density were obtained using random swim surveys in 1998 (Appendix B) and line transect surveys in 1999 (Appendix C). The proportion of the population removed was calculated as 2.66% (catch = 10 000 individuals) for 1998 and 15.33% (catch = 30 000 individuals) for 1999. These percentages equate to 105 of the 3974 abalone for 1998 and 735 of the 4797 abalone surveyed in 1999. To examine the response to a wide range of catch levels, and given the potential for error associated with the catch-by-numbers estimation, simulations were run for a range of catch-by-numbers for each year, namely, 105, 250, 500, 735, 1000, and 1400 individuals. The maximum catch limit of 1400 equalled the total number of legal-sized abalone in the 1998 surveyed population (the smaller of the two surveyed populations), where the proportion of legal-sized abalone was determined from length-frequency data. For 1998, before the fish-down, there were 733 legal-sized abalone in 2089 individuals measured, that is, 35.1% of the population was assumed to be of legal size, assuming that the survey was representative. For 1999, 827 of 2148 individuals measured were legal sized, or 38.5% of the population. The maximum catch limit is conservatively estimated as approximately 35% of 3974, the 1998 prefishing "population" size.

It is unreasonable to assume that each aggregation contains the same proportion of legal-sized individuals. The proportion of each aggregation to be removed by the simulated fishing (recall that legal length was 125–145 mm for the 1998 and 1999 fish-downs) was therefore determined stochastically based on aggregation-specific length–frequency data obtained for 188 aggregations during the April 1999 survey. The proportion of legal-sized abalone was calculated for each aggregation (single abalone were grouped by survey block; see Dowling et al. (2004) for a description of the survey design). A quantile–quantile plot of the proportions (over all aggregation sizes) showed them to be normally distributed. Given that there was no significant relationship between the proportion of legal-sized abalone in an aggregation and aggregation size (one-way analysis of variance: $F = 0.889$, df = 17,119, $\alpha(2) = 0.05$, $P = 0.588$), it was not necessary to consider different aggregation sizes independently. In the simulations, the proportion of fishable abalone in each aggregation was determined by random sampling from a normal distribution with mean = 0.409 and SD = 0.309 calculated from the April 1999 sampled aggregations. Random values >1 or <0 were assigned the values 1 and 0, respectively.

It was assumed that the difference in numbers at each aggregation size between the pre- and post-fishing surveys was due to fishing mortality. That is, during the 2 weeks of fishing between surveys, it was assumed that no reaggregation had occurred and that natural mortality was negligible, so that the postfishing surveyed aggregation distributions directly reflected the impact of fishing on aggregation structure.

In each simulation, abalone were randomly removed according to one of the three fishing strategies and compared with the specified catch limit. If the number removed was below this limit, the number of individuals or aggregations to be randomly selected was incremented by one. Fishing ceased when the number of individuals removed equalled or exceeded the specified catch limit. The aggregation frequency distribution (i.e., the proportion of individuals within each aggregation size) of the remaining individuals (the "post-fishing" simulated distribution) and the third moment of this distribution were then determined. The latter indicates the amount of skew in the distribution, with the sign of the third moment indicating the direction and the magnitude indicating its intensity. A highly positive skew indicates a higher proportion of individuals in larger aggregations.

Simulations were repeated 100 times and a plot of the resulting aggregation frequency distribution obtained for each fishing strategy – catch limit combination. The proportion, rather than the number, of individuals was used for ease of comparison across different catch limits. The average proportion of abalone in each aggregation size was calculated by dividing the average number of abalone in each aggregation across the 100 iterations by the sum of average total numbers over all aggregation sizes.

The mean of the estimates of the third moment, calculated from the 100 simulated distributions for each fishing strategy – catch limit combination, was compared with the third moment

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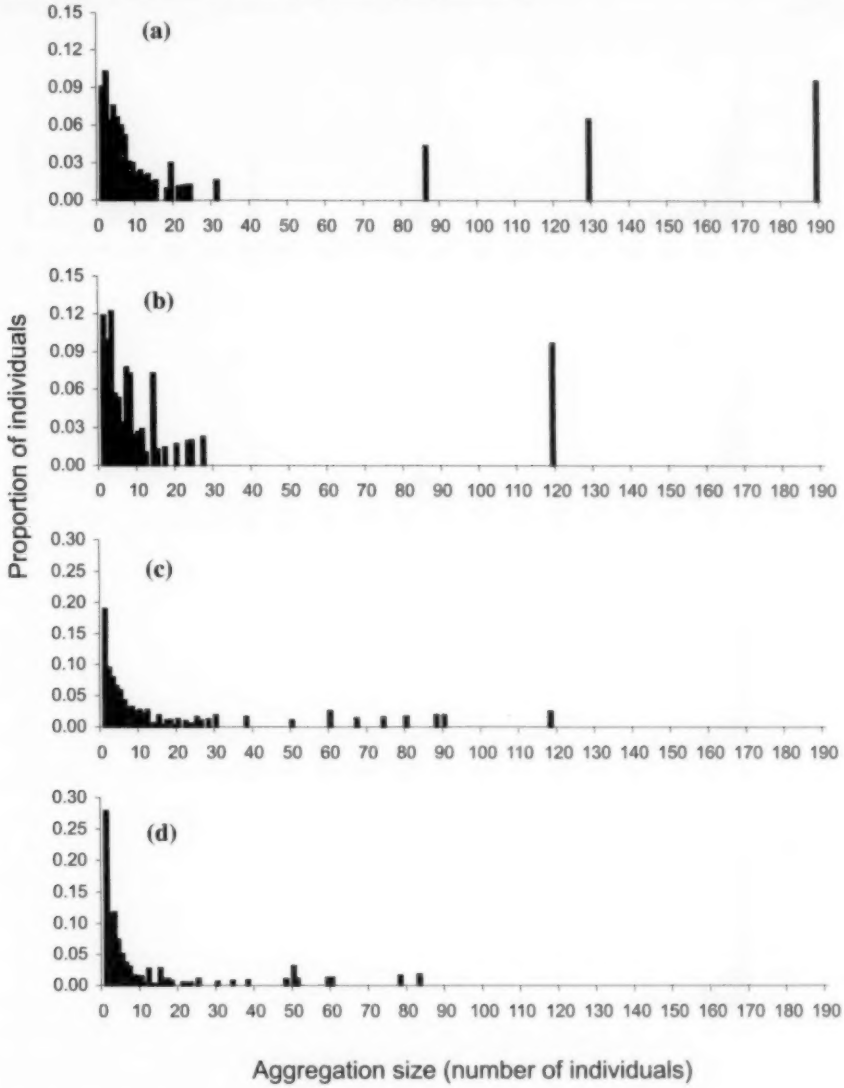
Fig. 1. Bar graphs of the 1998 (*a*) prefishing and (*b*) postfishing survey data and of the 1999 (*c*) prefishing and (*d*) postfishing survey data illustrating the proportion of individuals occurring in each aggregation size.



of the surveyed postfishing (May) aggregation frequency distribution using a one-sample *t* test. This test uses the standard error of the mean, calculated from the 100 estimates of the third moment, as a measure of the expected variability. Additionally, the aggregation frequency distribution for each of the 100 iterations was compared with the observed postfishing (May) aggregation distribution using a χ^2 test, where categories were the aggregation sizes (note that aggregation sizes were never combined). If more than five of the 100 simulated postfishing distributions were statistically different from the observed distribution, the fishing strategy being tested was concluded to have a different impact on the aggregation structure from that that had been observed. The χ^2 tests compared the overall shape of the aggregation frequency distributions, whereas the third moment *t* tests examined the skew in the distributions and were therefore more sensitive to the proportion of abalone in larger aggregations.

Results

Graphical output from fishing simulations

Varying catch levels had little effect on the overall aggregation frequency distribution patterns for each fishing strategy and year. Observable changes were continuous with respect to increasing or decreasing catch levels, and so, for comparison between strategies, only the frequency distributions for the minimum and maximum catch limits (105 and 1400) are presented. For comparison with the simulated output, the surveyed pre- and post-fishing aggregation frequency distributions for 1998 and 1999 are presented (Fig. 1).

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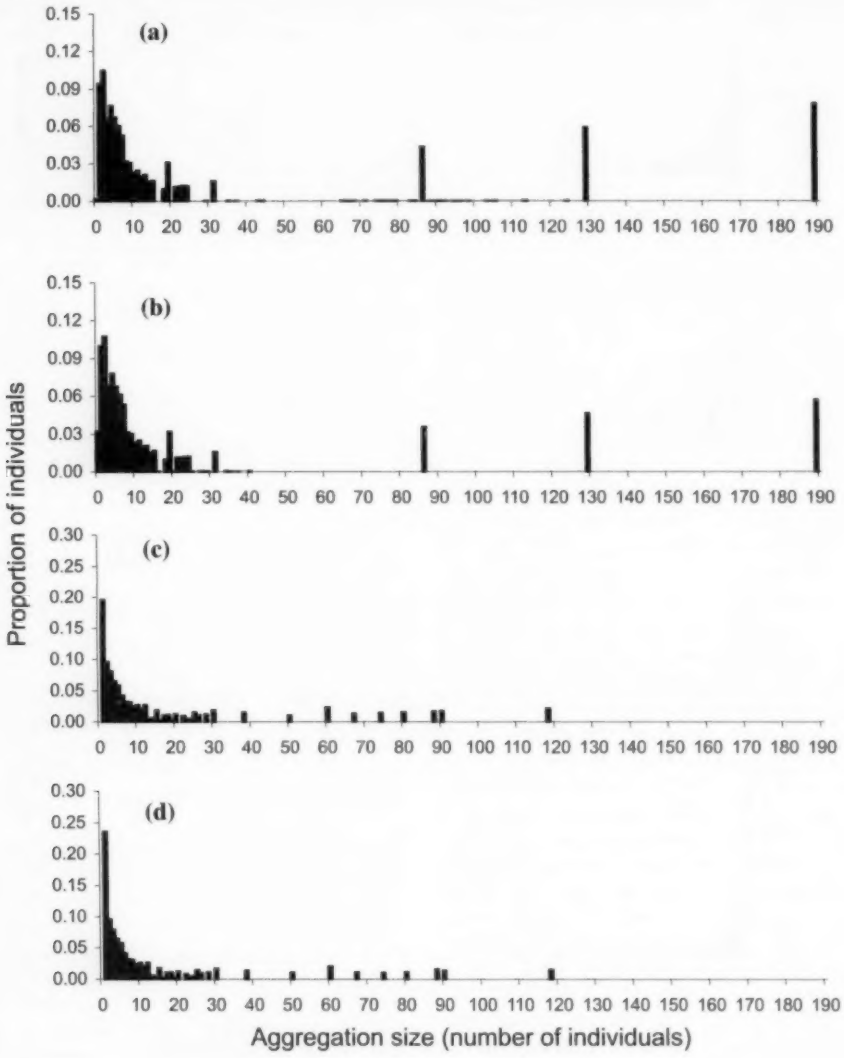
Fig. 2. Bar graphs of (*a* and *b*) 1998 and (*c* and *d*) 1999 simulation outputs for the most random fishing strategy illustrating the proportion of individuals occurring in each aggregation size. Simulated output is averaged over 100 simulations for catch limits (*a* and *c*) 105 and (*b* and *d*) 1400.



The most random strategy had little effect on the relative proportion of individuals in each aggregation size with respect to both the input aggregation distribution (April survey data) and increasing catch limits (Fig. 2). Increasing catch resulted in a slight decrease in the proportion of individuals in the three largest aggregations for 1998 (Figs. 2*a* and 2*b*), and for 1999, the highest catch limit (1400) resulted only in a very slight decrease in the proportion of individuals in the largest aggregation (Fig. 2*d*). The only other trend was an increase in the proportions of individuals in aggregations of size one with increasing catch limits. There was more positive skew (i.e., more larger aggregations) than the May (postfishing) survey aggregation distribution plots (Figs. 1*b* and 1*d*).

The second fishing strategy broke aggregations larger than 30 into numerous smaller aggregations of adjacent sizes (Fig. 3). For the lowest catch limit (105), these were immediately below the original aggregation size but became smaller as catch increased. For 1998, the average proportion of individuals in aggregations of approximately 15–30 decreased with increasing catch (Figs. 3*a* and 3*b*). Aggregations of 15–30 maintained the same relative proportion of individuals irrespective of the catch limit for the 1999 simulations (Figs. 3*c* and 3*d*), probably because the many larger aggregations for this year were broken down into aggregations whose sizes fell in this category. The proportion of individuals in aggregations of less than or equal to eight (for 1998) or four (for 1999) increased with increasing catch. Again, the simulated postfishing aggregation distributions show more positive skew than the May (postfishing) survey aggregation distribution plots (Figs. 1*b* and 1*d*).

The strategy most closely approaching targeted fishing had the greatest impact on the larger aggregations (Fig. 4).

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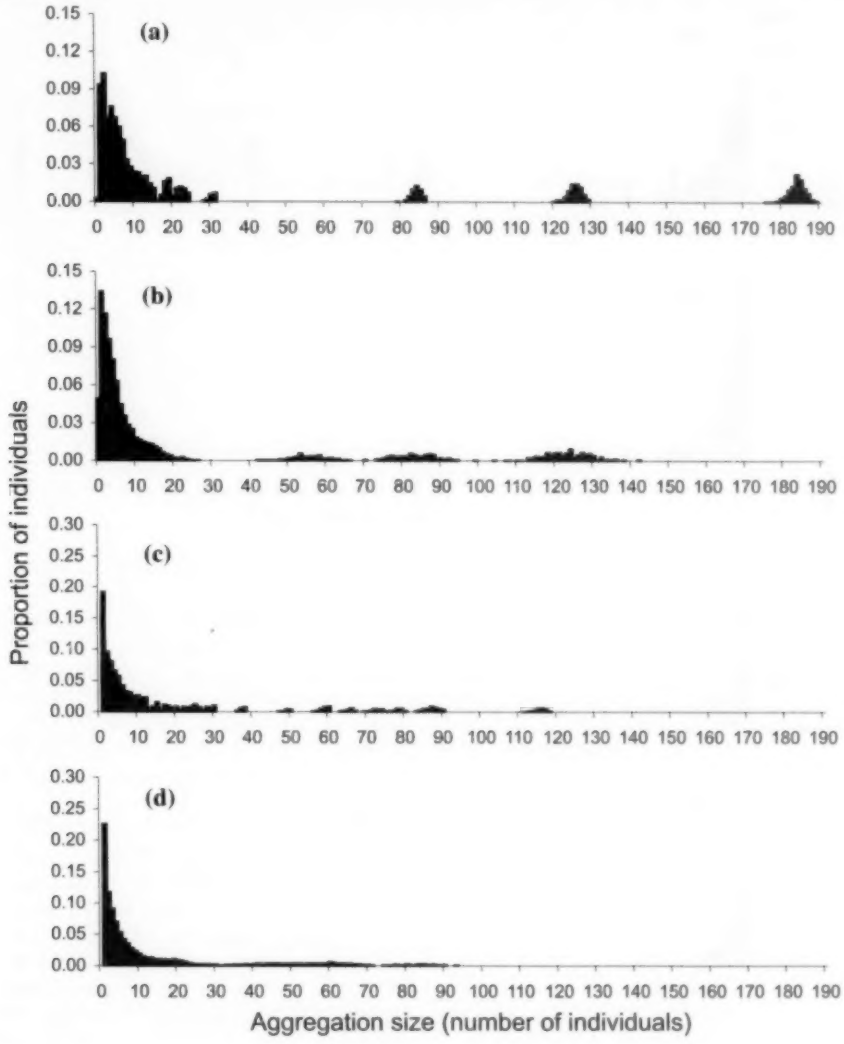
Fig. 3. Bar graphs of (*a* and *b*) 1998 and (*c* and *d*) 1999 simulation outputs for the intermediate random fishing strategy illustrating the proportion of individuals occurring in each aggregation size. Simulated output is averaged over 100 simulations for catch limits (*a* and *c*) 105 and (*b* and *d*) 1400.



The largest aggregations were first to become depleted with increasing catch limits, with a steady reduction in the relative average proportion of individuals in the three largest aggregations in 1998 (Figs. 4*a* and 4*b*) and in aggregations >20 in 1999 (Figs. 4*c* and 4*d*). The relative average proportion of individuals in aggregations from 9 to 30 (1998) or from 5 to 30 (1999) did not change as fishing increased, but there was a steady increase in the relative average proportion of individuals in smaller aggregations (less than nine (1998), less than five (1999)) (Fig. 4). The aggregation frequency distributions for this strategy most closely approximated the postfishing survey distributions in terms of shape and skew. In particular, the distributions corresponding to the catch limit of 1000 were visually the most similar to the surveyed postfishing aggregation frequency distributions in both years (Fig. 5).

In summary, the most random strategy showed the most positive skew in the simulated postfishing aggregation distributions, such that the larger aggregations were not being targeted, and little change with respect to catch limit, so that the randomness of selection results in the same average aggregation frequency distribution irrespective of the amount of catch. For the more targeted strategy, the relative average proportion of individuals was appreciably reduced in larger aggregations and increased in very small aggregations, reflecting a breakdown of larger aggregations into small fragmented ones.

χ^2 analyses

The χ^2 comparisons of the simulated and observed postfishing distributions of abalone in aggregation sizes yielded P values of zero for every iteration across all catch levels

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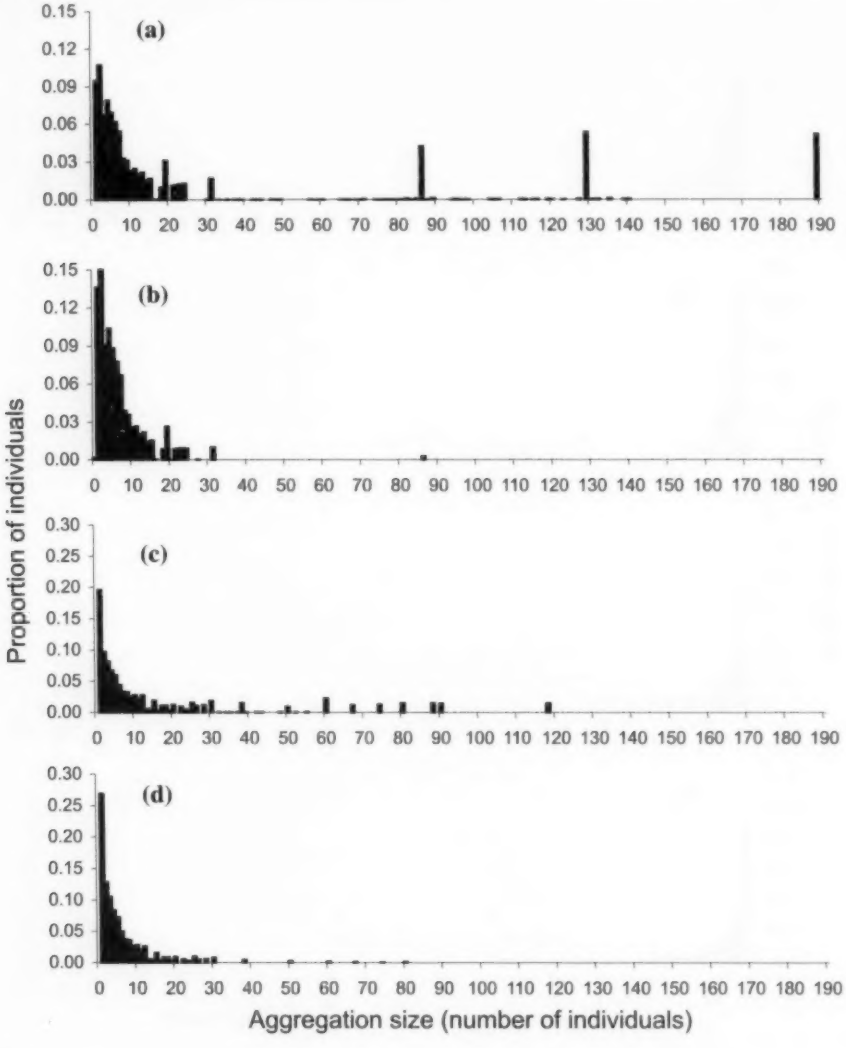
Fig. 4. Bar graphs of (*a* and *b*) 1998 and (*c* and *d*) 1999 simulation outputs for the most targeted fishing strategy illustrating the proportion of individuals occurring in each aggregation size. Simulated output is averaged over 100 simulations for catch limits (*a* and *c*) 105 and (*b* and *d*) 1400.



and fishing strategies. This strongly suggests that the aggregation frequency distributions obtained for each simulation iteration were highly significantly different from the postfishing survey distribution for that year in terms of their overall shape.

For both years, the minimum χ^2 value (728.49 for 1998, 467.14 for 1999) occurred in the simulations using the more targeted fishing strategy with the highest catch limit of 1400. It follows that the aggregation frequency distributions for the more targeted strategy and the highest catches were the least different from those of the postfishing surveys (although the null hypothesis of no significant difference was rejected). It should be noted that the χ^2 test is extremely powerful and as such detects small differences between distributions, particularly when N is large (N ranges from 2574 to 3869 in 1998 and from 3397 to 4692 for 1999).

Third moments indicating skew

Similar implications to the χ^2 results were found by comparing the amount of (positive) skew in the simulated and survey aggregation distributions. The null hypothesis that the mean third moment is equal to the third moment of the surveyed postfishing aggregation distribution was strongly rejected for every fishing strategy – catch limit combination in each year (Table 1). The P values were mostly zero and all were <0.01 (Table 1). The highest P value was 0.001 for the first strategy (that most closely approaching targeted fishing) and a catch limit of 500 in 1999 and 5.21×10^{-6} for the first strategy and a catch limit of 105 in 1998. Thus, this strategy yields aggregation frequency distributions whose skew most closely approaches that of the postfishing surveyed distributions. In both years, third moments were at a minimum (57.57 for 1998, 58.38 for 1999), indicating a lesser degree of skew for

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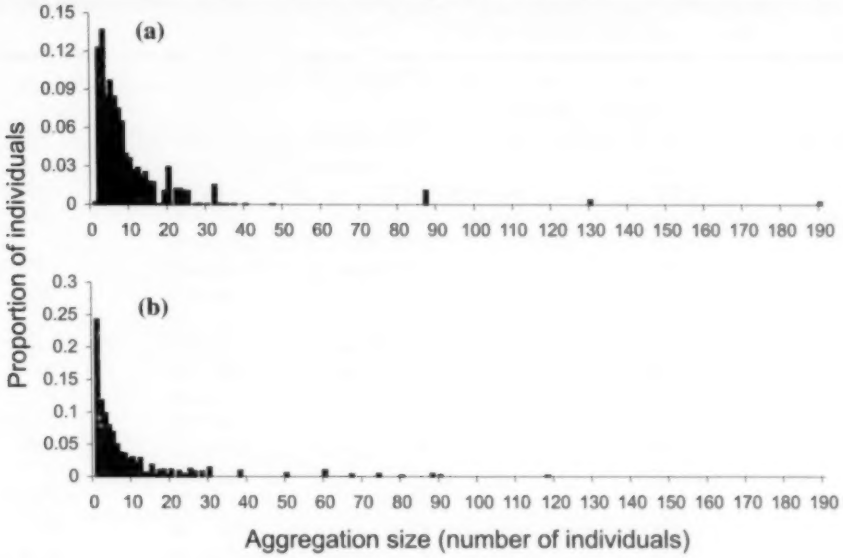
Fig. 5. Bar graphs of (*a*) 1998 and (*b*) 1999 simulation outputs for the most targeted fishing strategy illustrating the proportion of individuals occurring in each aggregation size. Simulated output is averaged over 100 simulations for catch limit 1000.



the more targeted strategy and a catch limit of 1400 (Table 2, 1998).

Mean third moments (across the 100 iterations) were also minimized (126.35 for 1998, 162.38 for 1999) for this fishing strategy and catch level (Table 2). Maximum mean third moments (22 939 for 1998, 2676.42 for 1999) indicated that the highest degree of positive skew occurred for the most random strategy and the lowest catch limit (105) (Table 2, 1998). The overall maxima across all iterations (28 290.46 for 1998, 2999.55 for 1999) occurred with the most random strategy and catch limits of 735 for 1998 and 250 for 1999.

For both years, the mean third moment consistently decreased with increasing catch for a given fishing strategy and was consistently lowest for the more targeted strategy and highest for the most random strategy across a given catch level. This implies that the more targeted strategy and higher catch limits have the greatest effect in reducing the proportion of individuals in larger aggregations, whereas the most random strategy has the least effect.

For the 1999 simulations, mean skew was lower than the postfishing survey distribution's skew for the highest three catch limits within the more targeted fishing strategy. Thus, these simulations were the only ones to reduce the proportion of individuals in larger aggregations more than the surveyed postfishing distributions. Recalling that the actual scaled catch-by-numbers was approximated to be 735, direct comparison of strategies for this catch limit shows that the more targeted strategy had a mean third moment only 25% less than the third moment from the survey, and the other more random strategies have much more positive skew. In 1998, the actual scaled catch-by-numbers was approximated to be 105, and at this catch limit, all strategies yielded aggregation distributions with greater skew. This suggests that the actual fishing had a greater impact on larger aggregations than that invoked by most of the simulations, especially those about the estimated catch-by-numbers.

Discussion

Simulations of alternative fishing strategies

There was consistent evidence that the observed postfishing aggregation frequency distributions could not have been achieved with a random fishing strategy. All of the strategies gave statistically significantly different results from the observed distributions for both χ^2 tests for the overall shape of the distributions and *t* tests for the third moments of the distributions. However, the more targeted strategy yielded bar graphs and third moments that showed the greatest reduction in the proportion of individuals in larger aggregations. Third moment *t* test *P* values were highest and χ^2 values lowest for the most targeted harvesting strategy, so that it most closely approximates the postfishing survey data. Conversely, aggregation frequency distributions from the most random strategy yielded the most skew, indicating minimal impact of this strategy on larger aggregations.

As such, the hypothesis that the observed postfishing aggregation structures are likely to result from random fishing was rejected. The more targeted simulated strategy, whereby larger aggregations have a higher probability of capture, more closely approached the true fishing behaviour across the two years. Surveyed and simulated distributions using the more targeted strategy suggested that the largest aggregations (>30) are broken down, aggregations from 5 to 30 apparently remain stable, and the proportion of abalone in the smallest aggregations (less than five) increases.

The χ^2 tests indicated that all of the simulated strategies, including that most closely approaching targeted fishing, yielded aggregation frequency distributions that were statistically different from the observed postfishing distribution. However, not all processes that explain aggregation behaviour have been modelled in these simulations, and so it should not be expected that the patterns between the modelled and observed postfishing distributions should show no significant difference.

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Table 1. Results of 1998 and 1999 one-sample *t* tests for the null hypothesis that the mean third moment across 100 iterations (for each catch limit and fishing strategy) is equal to the third moment of the surveyed postfishing aggregation frequency distributions (1998 H_0: third moment = 6818.84; 1999 H_0: third moment = 1000.44).

Catch limit (no. of greenlip abalone)	Summary statistics (100 iterations)	Simulated fishing strategy		
		Most random	Intermediate	Most targeted
1998				
1400	*t*	8.098	–133.072	–616.623
	df	99	99	99
	P	1.48×10^{-12}	0	0
1000	*t*	15.338	–56.264	–75.901
	df	99	99	99
	P	0	0	0
735	*t*	13.249	–10.767	–46.378
	df	99	99	99
	P	0	0	0
500	*t*	18.302	34.756	–23.072
	df	99	99	99
	P	0	0	0
250	*t*	32.009	111.323	–7.175
	df	99	99	99
	P	0	0	1.34×10^{-10}
105	*t*	38.952	223.013	4.819
	df	99	99	99
	P	0	0	5.21×10^{-6}
1999				
1400	*t*	10.897	8.756	–81.718
	df	99	99	99
	P	0	0	0
1000	*t*	18.169	59.274	–20.051
	df	99	99	99
	P	0	0	0
735	*t*	21.951	96.258	–6.250
	df	99	99	99
	P	0	0	1.04×10^{-8}
500	*t*	26.201	128.669	3.384
	df	99	99	99
	P	0	0	1.02×10^{-3}
250	*t*	36.604	229.667	15.448
	df	99	99	99
	P	0	0	0
105	*t*	50.182	353.379	33.886
	df	99	99	99
	P	0	0	0

The more targeted strategy may not adequately describe the nature of the targeting behaviour. For example, the selection probability for individuals in aggregations is not weighted to incorporate prior knowledge of the location of aggregations. This may partly account for the statistical difference between the distributions resulting from this strategy and the surveyed postfishing distributions. Additionally, the χ^2 test, as stated above, is very powerful, and as such, small differences between distributions are interpreted as significant. A less powerful test may have resulted in the acceptance of the null hypothesis for the more targeted strategy. Finally, the surveyed pre- and post-fishing aggregation distributions are not the result of an exhaustive census and so may not originate from a representative sample. The survey data are also prone to observation error, in terms of both failing to detect all of the individuals in a given aggregation and approximating the number of individuals in very large aggregations. Note that no transects are exactly repeated in the same or other years.

A major assumption for the least and most random strategies was that all legal-sized abalone in an aggregation are detected and removed. However, postfishing surveys have shown legal-sized abalone in aggregations. It is possible that these aggregations went undetected or that the abalone were cryptic and emerged in response to space generation from fishing. The stochastic method for allocating the proportion of legal-sized abalone to an aggregation allowed for variability

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Table 2. 1998 and 1999 summary statistics for third moments of aggregation frequency distributions from 100 iterations for each fishing strategy and catch limit.

Catch limit (no. of greenlip abalone)	Summary statistics (100 iterations)	Simulated fishing strategy		
		Most random	Intermediate	Most targeted
1998				
1400	Minimum third moment	235.91	2 742.04	57.57
	Maximum third moment	24 766.52	4 069.29	510.45
	Mean	11 664.86	3 310.70	126.35
	SD	5 983.89	263.63	108.53
1000	Minimum third moment	4 232.55	4 194.62	92.87
	Maximum third moment	27 634.52	5 739.57	4 744.38
	Mean	14 374.05	5 048.96	506.20
	SD	4 925.94	314.57	831.69
735	Minimum third moment	2 022.93	5 664.09	103.23
	Maximum third moment	28 290.46	7 404.56	6 086.99
	Mean	15 196.68	6 482.39	1 240.34
	SD	6 323.43	312.48	1 202.84
500	Minimum third moment	5 053.79	7 154.58	254.29
	Maximum third moment	28 052.75	8 856.66	6 102.37
	Mean	17 586.74	8 038.47	2 698.47
	SD	5 883.60	350.91	1 785.89
250	Minimum third moment	8 227.51	9 209.71	819.59
	Maximum third moment	27 905.92	10 628.32	10 298.39
	Mean	20 637.32	9 896.04	5 383.32
	SD	4 317.03	276.42	2 000.66
105	Minimum third moment	15 109.78	10 519.06	1 618.73
	Maximum third moment	27 791.97	11 546.41	11 602.77
	Mean	22 939.21	11 058.85	7 816.06
	SD	4 138.55	190.12	2 069.53
1999				
1400	Minimum third moment	269.46	902.76	58.38
	Maximum third moment	2 698.14	1 279.66	509.21
	Mean	1 649.10	1 071.17	162.38
	SD	595.25	80.78	102.56
1000	Minimum third moment	800.48	1 289.06	122.09
	Maximum third moment	2 977.60	1 692.97	1 321.64
	Mean	2 020.23	1 498.88	472.74
	SD	561.27	84.09	263.17
735	Minimum third moment	665.15	1 621.58	194.10
	Maximum third moment	3 016.92	2 057.51	1 979.45
	Mean	2 142.28	1 810.19	759.38
	SD	520.17	84.12	385.70
500	Minimum third moment	1 181.65	1 927.86	187.48
	Maximum third moment	3 009.82	2 321.51	2 485.11
	Mean	2 260.91	2 135.79	1 168.01
	SD	481.08	88.24	495.15
250	Minimum third moment	1 406.51	2 385.43	788.94
	Maximum third moment	2 999.55	2 754.61	2 804.93
	Mean	2 508.82	2 550.47	1 757.87
	SD	412.08	67.49	490.33
105	Minimum third moment	1 684.08	2 652.78	1 152.29
	Maximum third moment	2 992.51	2 901.32	2 911.15
	Mean	2 676.42	2 784.87	2 240.02
	SD	333.98	50.50	365.81

Note: The third moment is 6818.84 for the May 1998 survey data and 1000.44 for the May 1999 survey data.

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in the legal proportion of abalone in each aggregation. However, given the degree of camouflage for greenlip abalone, it would have been preferable to have also assigned a stochastic proportion, for example, between 80% and 100%, of those legal-sized abalone that would be detected and removed from each aggregation.

A second assumption was that abalone had no opportunity to reaggregate in the time between fishing and surveying. The possibility that abalone may have reaggregated before the postfishing surveys or that cryptic juveniles may have emerged and so enlarged aggregations must be considered. There is evidence from the surveys for emergence of small (sublegal) abalone after fishing but not in so large a quantity as to affect the overall aggregation structure. Strong reaggregation is unlikely to occur in the time frame of 2 weeks between the commencement of fishing and the postfishing survey, given Shepherd and Godoy's (1989) mean and maximum movement rates, albeit for juveniles, of 0.5 and 1.2 $m \cdot month^{-1}$, respectively.

Additionally, movement with respect to crevice abundance in relocated adults in Waterloo Bay (Shepherd 1986) showed that, when removed from crevices, abalone moved <20 m at one site (C3) and 25–30 m in another (C4) over 6 months, but movement was negligible where crevices were abundant. It was assumed that the fished abalone aggregations would be stable with respect to desired habitat and thus would not demonstrate the movement patterns described by Shepherd (1986). This would probably be especially true for larger aggregations, which may be large as a direct consequence of the presence of a large patch of desirable habitat. Regardless, by surveying immediately after the 2-week fish-down, even acknowledging that most fishing takes place in the first 3–4 days of the opening, abalone have only 1–2 weeks at liberty before the bay is resurveyed. Given the above movement rates, significant reaggregation would not be anticipated in this time. Natural mortality would also reasonably be assumed to be negligible over this time period.

It should be noted that the spatial distribution of aggregations is not considered in the simulations. It is indirectly implied that aggregations are randomly (haphazardly) distributed on the bottom. This does not take into account that some aggregations may occur in areas in which less effort was expended (because of poor visibility, preconceptions of areas of abundance, etc.). It is also known that greenlip abalone aggregations are found in crevices at the sand–limestone interface. Given the evidence that divers search "good bottom" and are restricted by visibility, the random fishing strategies being simulated may not be realistic or conceivable. However, this is not such a contentious issue given that the simulations are addressing a theoretical question: that of the possibility of achieving similar aggregation frequency distribution patterns by random fishing over aggregations.

In summary, these simulations provide an independent validation that the postfishing aggregation frequency distributions obtained from surveys in 1998 and 1999 could not have resulted from random search behaviour by divers. The postfishing survey data are most likely to be a direct representation of the impact of targeted fishing on larger aggregations on the overall aggregation structure of the greenlip abalone population. These data can therefore be used to quantify targeted fishing behaviour in terms of aggregation-specific catch patterns (e.g., determining an aggregation-specific catchability) and the response of aggregations to targeted fishing.

Aggregation structure appears to be a critical factor affecting population sustainability, not only for greenlip abalone in Waterloo Bay but potentially for other species. For *Halitois iris* populations, large aggregations are relatively infrequent and most aggregations are of size less than five (McShane 1998). However, large aggregations determine the overall abundance of the population (McShane 1995). Targeting large aggregations of *H. iris* can have a relatively low impact on the total number of aggregations but a large impact on the number of individuals (McShane 1996). The importance of aggregation structure with respect to fishing behaviour also has relevance for other free-spawning benthic fisheries such as scallops and sea urchins. In these fisheries, the spatial distribution of spawning conspecifics, such as persistent or intermittent aggregations, as well as the abundance and size of individuals play an important role in reproductive success (Claereboudt 1999). The mechanisms modifying the spatial distribution of a species that rely on the broadcast gametes in the water column to ensure fertilization are thus likely to affect the effectiveness of this mode of reproduction (Claereboudt 1999). Thus, the targeting behaviour of harvesters, the ability of the population to reaggregate, and the relationship between aggregation size and fertilization success are all of importance in managing these fisheries. It is therefore important that population dynamics be described in aggregation-specific terms. These analyses have provided a basis to proceed with certainty towards such a description for the Waterloo Bay greenlip abalone population.

Acknowledgments

The authors wish to thank Dr. Scoresby Shepherd, who generously assisted with the design and implementation of the fieldwork and gave much advice during the development of this paper. Dr. Jeremy Prince and two anonymous reviewers provided helpful criticism of the manuscript. This work was undertaken as part of a Ph.D. study funded by an Australian postgraduate award.

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Appendix A. Calculating catch-by-numbers

Catch was recorded by weight and not absolute numbers, as it is impractical to count individual abalone for every diver, and moreover, most divers shell at sea and have their catch ready for transportation to the cannery on returning. As such, an estimate of total catch-by-numbers was made based on the length–weight relationship published for Waterloo Bay greenlip abalone by Shepherd and Baker (1998). The following procedure was used.

Known quantities were as follows.

C_w, total weight (kilograms) of abalone removed; calculated by multiplying the quota by the number of participating licences.

$\{x_i, i = \text{legal sizes}\}$, proportion of the average number of individuals captured in each 5-mm length bin. The average number in each length class was obtained from samples of the catch taken from different divers. The samples were assumed to be representative of the entire catch. In 1998, all shells from four divers were measured; in 1999, samples of approximately 50 shells from three divers were measured.

$\{w_i, i = \text{legal sizes}\}$, average weights at length for each 5-mm size class calculated using the relationship $W = aL^b$, where $a = 2 \times 10^{-4}$ and $b = 2.92$ (Shepherd and Baker 1998).

Assuming that the length–frequency data are taken from a representative sample, then it follows that

$$\text{(A1)} \quad C_{ni} = C_n x_i$$

where C_{ni} is absolute catch-by-numbers in length class i and C_n is absolute catch-by-numbers, the desired quantity.

Total catch-by-weight can then be rewritten as

$$\text{(A2)} \quad C_w = \sum_i C_{ni} w_i$$

and by substitution of eq. A1:

$$\text{(A3)} \quad C_w = \sum_i C_n x_i w_i = C_n \sum_i x_i w_i$$

Equation A3 is then rearranged to solve for C_n:

$$\text{(A4)} \quad C_n = C_w / \sum_i x_i w_i$$

Appendix A reference

Shepherd, S.A., and Baker, J.K. 1998. Biological reference points in an abalone fishery. *In* Management of marine invertebrate stocks. *Edited by* G.S. Jamieson. *In* Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. *Edited by* G.S. Jamieson and A. Campbell. Can. Spec. Publ. Fish. Aquat. Sci. No. 125. pp. 235–245.

Appendix B. Density estimates from timed random swim data

Densities were estimated from the timed random swim data using the formula of Shepherd (1985):

$$\text{(B1)} \quad D = \frac{1}{n} \sum_{i=1}^{n} \frac{N_i}{(E_i A_i)}$$

where N_i is the number of abalone measured, E_i is the searching efficiency of the ith diver, A_i is the area searched by the ith diver, and n is the number of replicates.

The area searched is related to swimming time by

$$\text{(B2)} \quad A_i = Tr_i - m_i r_i N_i + a_i d$$

where T is the diving time in minutes, m_i is the measuring time for an abalone, r_i is the power of the diver (square metres per minute), a_i is a difficulty constant representing the extent to which the power of the diver is affected by swell and algal density and so always has a negative value, and d is the difficulty coefficient for detecting abalone at

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different sites according to surge and algal cover, ranging from 0 in calm conditions with no algal cover to 4 in strong surge with high algal cover (Shepherd 1985). The measuring time and difficulty constant were estimated for the 1998 and 1999 surveys using average values from divers calibrated in previous years. Densities were calculated using both the calibrated values and averages from previous years for searching efficiency and power.

The density estimate for each site was divided by the area of abalone habitat in each site (obtained from S.A. Shepherd, SARDI Aquatic Sciences, P.O. Box 120, Henley Beach, South Australia 5022, Australia, personal communication), and the resulting values were summed to give an overall average for the bay. Since not all 20 blocks were surveyed, this value was divided by the proportion of the bay that was surveyed to standardize the overall density.

Appendix B reference

Shepherd, S.A. 1985. Power and efficiency of a research diver, with a description of a rapid underwater measuring gauge: their use in measuring recruitment and density of an abalone population. *In* Diving for Science 85. *Edited by* C.T. Mitchell. American Academy of Underwater Science, La Jolla, Calif. pp. 263–272.

Appendix C. Density estimates from line transect data

The software DISTANCE by S.T. Buckland et al. (publicly available on the World Wide Web at http://www.ruwpa.st-and.ac.uk/distance/) was used to obtain estimates of overall density from the line transect data. Distance sampling theory accepts that a large proportion of abalone may go undetected but allows accurate estimates of density to be made under the assumption that all objects directly under the transect line are censused (Buckland et al. 1993). A histogram of the detection frequency for each 0.5-m distance category is plotted. If all abalone were detected, this histogram would show, on average, a uniform distribution. Usually, however, detectability decreases with increasing distance from the transect line (Buckland et al. 1993), suggesting that a "correction factor", based on the distance data, is needed to account for undetected abalone. Underlying this theory is the concept of a detection function, which is fitted to the histogram:

$$g(y) = P\{\text{detection} \mid \text{distance } y\}$$

where y is the perpendicular distance from the transect line.

The DISTANCE software fits this detection function using a specified "key function" and "series expansion" (Buckland et al. 1993). A key function describing the shape of the histogram is selected based on visual inspection, and a flexible series expansion function is chosen to improve the fit of the key function to the distance data. In the case of the Waterloo Bay data, half-normal key functions and cosine series expansions were used.

The proportion of abalone detected is obtained by integrating the detection function from 0 to the maximum perpendicular distance category. The inverse of this proportion is the correction factor. The correction factor is applied to the total number of individuals detected to give an estimate of the total number of abalone in the area surveyed (Buckland et al. 1993). This number divided by the area gives the density. These calculations are performed automatically by the DISTANCE software. The Waterloo Bay line transect data were pooled to give a single detection function, from which the overall density of greenlip abalone was derived. Densities for survey blocks with adequate data to generate a detection function were also obtained by pooling the replicates within the block.

Appendix C reference

Buckland, S.T., Anderson, D.R., Burnham, K.P., and Laake, J.L. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, U.K.

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Drifters versus residents: assessing size and age differences in Atlantic salmon (*Salmo salar*) fry

Valérie Bujold, Richard A. Cunjak, Jason P. Dietrich, and David A. Courtemanche

Abstract: Some young-of-the-year Atlantic salmon (*Salmo salar*) have a tendency to drift soon after emergence from the gravel, whereas others, called resident fry, set up and defend territories. Little is known about the mechanisms regulating this strong tendency to drift soon after emergence, a phenomenon that can greatly influence survival within a population. This study was carried out in the Western Brook system, Gros Morne National Park, Newfoundland, Canada. The objective was to assess differences, through biometric characteristics, between drifting and resident Atlantic salmon fry by examining both groups of fish caught simultaneously in the same riverine habitat. Resident salmon fry can be up to 4.8% longer and 20.4% heavier compared with drifting fry of similar age (measured in days since emergence). Therefore, it seems that competition, more than prior residence effect, could be part of the driving forces behind this active movement and that differences between subpopulations of Atlantic salmon fry can have major repercussions on life history patterns.

Résumé : Certains des jeunes saumons de l'Atlantique (*Salmo salar*) de l'année ont tendance à dériver peu après leur émergence du gravier, alors que d'autres, les alevins résidants, établissent et défendent des territoires. On connaît peu les mécanismes responsables de cette forte propension à la dérive peu après l'émergence, un phénomène qui peut grandement influencer la survie au sein de la population. Notre étude a été réalisée dans le système hydrographique de Western Brook, parc national du Gros Morne, Terre-Neuve, Canada. Son objectif était d'évaluer les différences dans les données biométriques entre les alevins du saumon de l'Atlantique qui dérivent et ceux qui restent sur place en comparant les deux groupes de poissons capturés simultanément dans le même habitat de rivière. Les alevins résidants peuvent être jusqu'à 4,8 % plus longs et 20.4 % plus lourds que les alevins de même âge (jours depuis l'émergence) en dérive. Il semble donc que la compétition, plus que l'effet de première occupation, puisse être l'un des facteurs explicatifs importants de ce déplacement actif et que des différences entre les sous-populations d'alevins du saumon de l'Atlantique puissent avoir des répercussions majeures sur la structure du cycle biologique.

[Traduit par la Rédaction]

Introduction

Salmonid populations in streams are often assumed to be limited by the space available for feeding territories of juveniles (Chapman 1966; Allen 1969). The chances of a young fish surviving depend heavily on its ability to compete and defend an area within its natal stream (Elliot 1990*a*, 1990*b*; Titus 1990). Individuals not acquiring a territory are presumably displaced downstream (Chapman 1962; Mason and Chapman 1965) or die (Elliot 1990*a*, 1990*b*; Brännäs 1995). Moreover, the mortality or downstream dispersal of the individuals that are unable to acquire territories is widely accepted as the main method of population regulation among young salmonids (Crisp and Hurley 1991).

It is known that some young-of-the-year (0+) Atlantic salmon (*Salmo salar*) tend to drift soon after emergence from the gravel, whereas others, so-called resident fry, set up and defend territories. The downstream movement of salmon fry is greater during darkness (Kennedy and Stange 1986; Heggenes and Traaen 1988), and the majority of fry remain close, within less than 1 km downstream, of the redd site (Kennedy and Stange 1986; Marty and Beall 1989; Webb et al. 2001). Dispersal from redds is one of the most important periods in the early life of Atlantic salmon, and the factors influencing the distribution of salmonid fry from redds are poorly understood (Heggenes 1990). By emigrating from densely populated areas, young fry have a chance to obtain a profitable individual territory that can provide them with a feeding site and shelter (Mikheev et al. 1994). The most intensive dispersal of 0+ salmon occurs during the 2 months after emergence (Beall et al. 1994).

According to the literature, there are two waves of downstream dispersal in Atlantic salmon fry (Marty and Beall 1989; Johnston 1997). The first wave of dispersal, immediately after emergence, might be expected because it is a method by which the aggregated population around redds can be dis-

Received 4 October 2002. Accepted 7 September 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 31 March 2004.
J17129

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 doi: 10.1139/F03-162 © 2004 NRC Canada

persed to maximize use of available habitat and to potentially locate more productive zones downstream (Marty and Beall 1989; Crisp and Hurley 1991). The second dispersal wave, 10–20 days after emergence, is called the drifting movement (Marty and Beall 1989; Johnston 1997). This wave comprises later-emerging fry that are displaced by territorial intraspecific competition and forced to seek new territories downstream (Marty and Beall 1989; Johnston 1997). According to Johnston (1997), these fish would be expected to be smaller than those that hold territories successfully. By contrast, other researchers have found that those 0+ salmon fry readily drifting downstream during experiments were of larger than average size (Ottaway and Clarke 1981). However, differences between drifters and residents have never been specifically assessed in the wild.

Are drifting fry moribund? Are they bigger or smaller than resident fry? Is competitive ability the major factor responsible for the behavioural difference, or is it a matter of early emergence advantage? Early-emerging fry (or older fry) would be expected to dominate later-emerging fry because of their advantage in having first choice of favourable stream positions (Metcalfe and Thorpe 1992; Brännäs 1995; O'Connor et al. 2000), resulting in faster growth and lower mortality than those emerging and dispersing later because of the size advantage they should gain (Chapman 1962; Titus 1990; Brännäs 1995). According to Huntingford and García de Leániz (1997), the prior residence effect, whereby an animal that arrives first at a specific area gains a competitive advantage over subsequently arriving rivals, has been documented in a number of animal groups.

The main objective of this study was to assess the differences between drifting and resident Atlantic salmon fry, in the wild, by using biometric characteristics such as length, weight, and age. The project was also done to begin to understand the mechanisms regulating the downstream movement of wild salmon fry.

Materials and methods

The study was carried out in Western Brook and its tributary, Stag Brook, in Gros Morne National Park, Newfoundland, Canada (Fig. 1). The Western Brook system (49°44′N, 57°46′W) is located in the north end of the National Park and has a drainage basin of 194 km^2 (Hickey 1983). This large river system includes a deep fjord pond, Western Brook Pond (Fig. 1*b*). More than 20 streams flow into Western Brook pond, but most of them cascade off the steep cliffs of the fjord surrounding the eastern end of the lake. Stag Brook, located in the southwestern part of the lake, is the largest tributary and the only one occupied by salmonid species. This stream is about 9 km long and contains important spawning and juvenile rearing habitat but few staging areas for adult salmon (Anions 1994). Western Brook, approximately 5 km long, empties into the Gulf of St. Lawrence and is recognized for its good rearing habitat for juveniles (36% riffle area) and some large steadies and pools where adults can stay (Hickey 1983) (Table 1).

In this system, in addition to Atlantic salmon, anadromous and resident forms of brook trout (*Salvelinus fontinalis*) are present. Other fish species are threespine stickleback (*Gasterosteus aculeatus*), American eel (*Anguilla rostrata*), alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), and Arctic char (*Salvelinus alpinus*).

The initiation of sampling was set to precede the expected date of Atlantic salmon emergence by at least several days. Fish drift samplers were set and monitored daily from 2 June to 7 July 1999 in Stag Brook and from 9 June to 19 July 1999 in Western Brook. Each stream was sampled in a single location (Fig. 1*b*). The selection of sampling sites was based on preliminary research that identified locations where drifting fry were likely to be captured (V. Bujold, unpublished data) and were located near the mouths of both streams. Site selection also considered accessibility and stream sections where the river flow was naturally constricted. Drifting fish were sampled using drift samplers similar to those used by Johnston (1997). These drift samplers had a galvanized metal mouth-reducing cone that was round in cross section (diameter = 235 mm). Attached to the downstream end of the cone was a 1.3-m-long net (800-µm mesh). A removable collection bottle with 200-µm-mesh windows was attached to the end of the net with a hose clamp (see Johnston 1997). Three of these samplers were placed equidistantly across a transect of Western Brook and two in Stag Brook with the centre of the mouth adjusted daily at approximately 60% of the depth (the vertical point that represents the average water velocity for the water column). Samplers were attached with wire to steel posts driven into the riverbed.

Sampling for drifting and resident groups of fry began as soon as the first drifting fry were observed in the traps. In 1999, this occurred in mid-June for Stag Brook but not until the end of June in Western Brook. Our goal was to sample comparable resident and drifting fry simultaneously. Resident fry were captured by electrofishing, whereas drifting fry were collected with drift samplers, within the same riffle habitat. A 30-m-long block net (6-mm mesh) was placed immediately downstream of the drift samplers to preclude drifting fry from passing in the area where electrofishing was to be carried out. The block net was put in place before dusk and removed after all of the fish were captured. The sampling was done at night because drifting movement is mostly nocturnal (Marty and Beall 1987; Bardonnet 1993; Heland et al. 1995) and the duration of the electrofishing sampling averaged 20 min in Stag Brook and 25 min in Western Brook. It was assumed that fish caught by electrofishing were destined to be resident and not drifters and that for each sampling period of this study, fry could not escape from the net because of the trap design, water velocity, and water temperature (V. Bujold et al., unpublished data).

In Western Brook, fry movement started around 0030 and around 2330 in Stag Brook. We sampled every 3 days, at each site, until the end of the drifting movement to establish any variation in time (five sampling periods in Stag Brook and four in Western Brook). In Western Brook, there was an 8-day delay between the first and second sampling periods because of a slow start in the fry drifting movement. In each site and for every sampling period, we attempted to capture 20 fry from each "group"; these were retained and frozen for subsequent analysis.

Water temperature was recorded hourly within each stream using a thermograph (VEMCO®, Shad Bay, N.S.) set in the stream near the sampling site. Daily average water temperature was calculated.

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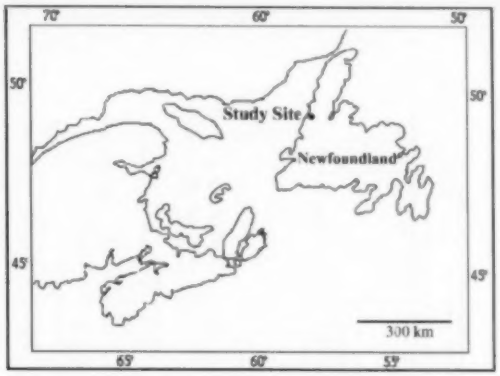
Fig. 1. Location of (*a*) Gros Morne National Park in Newfoundland, Canada, and (*b*) the Western Brook system showing the sampling sites.

(a)



(b)

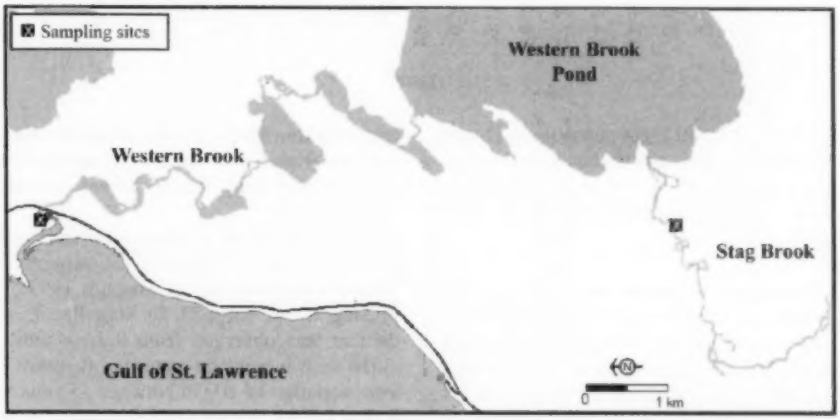


Table 1. Length, mean width, total area, and relative occurrence of major habitat type in Western Brook and Stag Brook (Hickey 1983).

			Area (m^2) and percent occurrence of each major habitat type				
	Length (m)	Mean width (m)	Rapids	Riffle	Run	Flat	Total area (m^2)
Western Brook	5388	48.5	8 578 (3%)	94 170 (36%)	71 607 (27%)	88 091 (34%)	262 446
Stag Brook	9504	18.3	71 255 (42%)	8 570 (5%)	73 764 (43%)	16 740 (10%)	170 329

Length, weight, and condition factor

All captured fry where measured for fork length in a standardized manner to the nearest millimetre with vernier callipers. They were placed on blotting paper for approximately 2 s on each side to remove excess water and weighed to the nearest milligram. Fish were then packed in aluminium foil, individually labelled, and frozen for subsequent otolith extraction.

Condition factor (K) was calculated using the following function:

$$K = (\text{body weight (g)}/\text{fork length (mm)}^3) \times 10^5$$

Age

Otoliths of each sampled fish were used to establish the age in days since emergence. All collected Atlantic salmon fry were dissected and the sagittal otolith (the largest otolith) was removed. Otoliths were mounted on standard glass microscope slides with thermoplastic glue (Crystalbond®) with the sulcal surface of the otolith facing upward (Secor et al. 1992). All of the otoliths were polished with fine 3-μm micropolishing film (3M®) to enhance the visibility of the microstructures. Preparations were viewed using a compound microscope that was linked by a high-resolution video camera to a video monitor and a computer to save as picture files for later use. Of the total 355 fry collected and assessed for age, 55 (16%) of the otoliths were excluded because clear images could not be obtained using the microscope or because otoliths were lost or damaged during dissection and polishing. All of the otoliths were read blind twice by the reader. When the second reading was different, the otolith was read a third time. For validation, a subgroup of the otoliths was read blind by other experienced readers.

The timing of emergence coincides with the onset of exogenous feeding in Atlantic salmon fry (Dill 1977; Northcote 1978). Age in days since emergence from the gravel was calculated for both groups (residents and drifters) based on the identification of the "check ring" at first feeding coinciding

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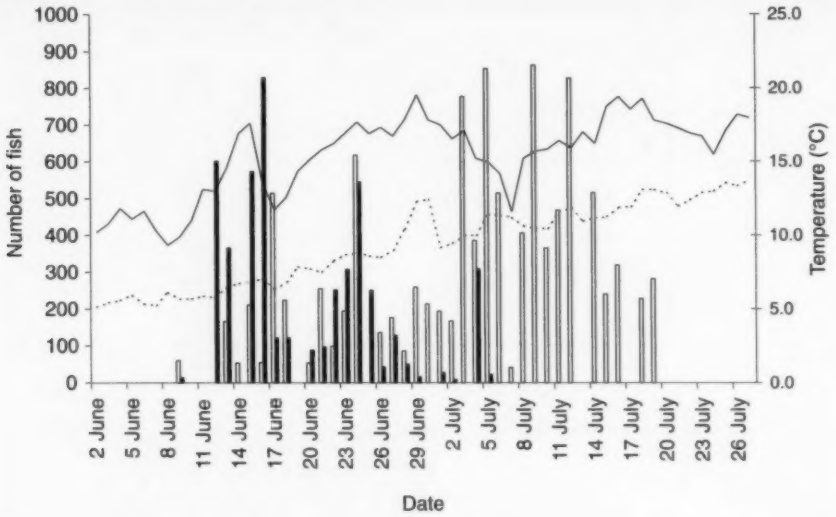
Fig. 2. Pattern of Atlantic salmon fry drift during the spring of 1999 in relation to water temperature in Stag Brook (solid line and solid bars) and Western Brook (broken line and open bars).



with emergence (Wright et al. 1991) and subsequent counts of daily otolith rings on the sagittal otolith because Atlantic salmon fry produce daily increments on their sagittae (Wright et al. 1991). Emergence date could thus be estimated.

Statistical analysis

A *t* test was used to compare the mean water temperature during spring and summer of 1999 between Stag Brook and Western Brook. To assess differences between drifters and residents, biometric characteristics were statistically compared using a two-way analysis of variance (ANOVA) to test for differences within each stream, using group (drifters or residents) and sampling periods as factors. Means for every characteristic were then compared between groups for each sampling period using a multiple comparisons test (Tukey–Kramer test). Homogeneity of variances and normal distribution were verified in every case.

One-way ANOVA was used to test the significance of the difference in emergence date frequency between the two streams. A correlation was conducted to establish the strength of the relationship between time and age since emergence, both in days.

Results

Patterns of Atlantic salmon fry drifting movement were different in Western Brook and Stag Brook. Drifting movement began at the same date within each brook, on 9 June 1999, but ceased after 26 days in Stag Brook (5 July) and 40 days in Western Brook (19 July) (Fig. 2). Drifting movement was more protracted in Western Brook where 56% of the drifting movement occurred over a 12-day period (from 3 July to 14 July), whereas in Stag Brook, 57% occurred over a 9-day period (from 11 June to 19 June).

These differences in drift timing are probably related to the respective water temperature in each stream during this period. From 2 June to 19 July 1999, there was a significant difference ($t = 12.78$, $P < 0.0001$, $n = 41$) in mean water temperature, Stag Brook being warmer with temperature ranging from 9.3 to 19.5 °C compared with Western Brook where water temperature ranged between 5.1 and 13.1 °C (Fig. 2).

In general, drifting movement was variable over time. Distinctive waves of dispersal, as expected from the literature (Marty and Beall 1989; Johnston 1997), were apparent only in Stag Brook (Fig. 2). In Stag Brook, a first movement of drifters was observed from 9 June until 18 June and coincided with increasing water temperature and a peak in water level variation of 10 cm between 15 June and 16 June (Fig. 3). It was followed by a second wave of drift taking place from 20 June until the end of the drifting movement (Fig. 2).

Length, weight, and condition factor

Significant differences between resident and drifting Atlantic salmon fry were found for both length and weight in Western Brook (length: $F = 6.969$, df = 1, $P = 0.0091$; weight: $F = 8.249$, df = 1, $P = 0.0046$) as well as in Stag Brook (length: $F = 15.280$, df = 1, $P = 0.0001$; weight: $F = 10.04$, df = 1, $P = 0.0018$) (Fig. 4). For both length and weight, there was no significant interaction effect between the two factors (group and period) within the two brooks.

In Western Brook, resident fry were, on average, 4.8% longer and 20.4% heavier than drifting fry (Table 2; Fig. 4). Multiple comparison tests (Tukey–Kramer) established a significant difference between groups for length, when each of the sampling periods was separately analysed, for 8 July (-2.287_{avg}, 1.844_{crit}, $P < 0.05$) and 12 July (-1.375_{avg}, 1.309_{crit}, $P < 0.05$). For weight, resident fry were significantly heavier on 5 July (-0.056_{avg}, 0.048_{crit}, $P < 0.05$), 8 July (-0.089_{avg}, 0.067_{crit}, $P < 0.05$), and 12 July (-0.059_{avg}, 0.050_{crit}, $P < 0.05$). On average, in Stag Brook, mean length of resident fry was 3.3% longer than drifters and 12.2% heavier (Fig. 4). Multiple comparison tests established a significant difference for length only on 23 June (-0.908_{avg}, 0.669_{crit}, $P < 0.05$). A significant difference was also found for weight on 20 June (-0.060_{avg}, 0.036_{crit}, $P < 0.05$).

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Fig. 3. Water level variation in Stag Brook (solid line) and Western Brook (broken line) in 1999.

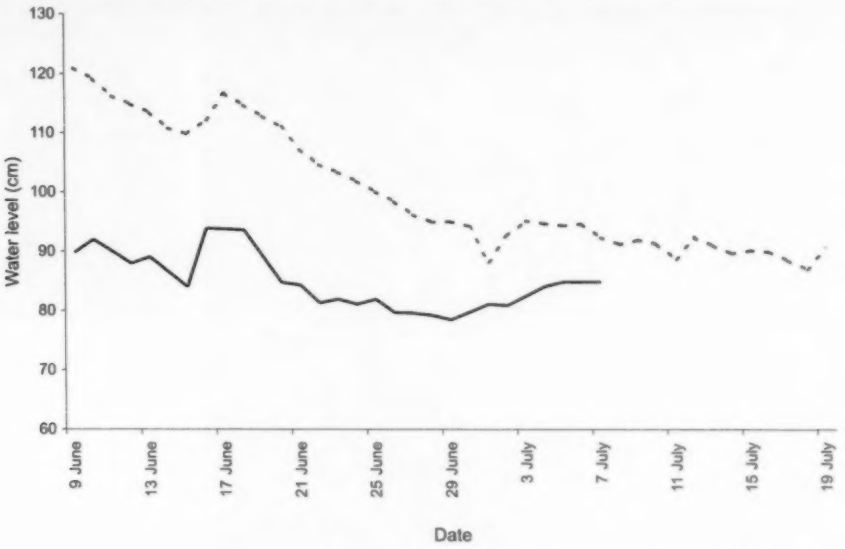

Table 2. Data on sampled drifting and resident Atlantic salmon fry during 1999 in Stag Brook and Western Brook.

				Average			Standard deviation		
Date	Brook	Fish group	*n*	Fork length (cm)	Weight (g)	Condition factor	Fork length (cm)	Weight (g)	Condition factor
17 June	Stag	Drifter	21	27.7	0.19	0.88	1.55	0.05	0.15
17 June	Stag	Resident	10	28.4	0.21	0.90	1.51	0.05	0.09
20 June	Stag	Drifter	30	27.6	0.19	0.90	1.59	0.05	0.14
20 June	Stag	Resident	10	28.7	0.25	1.06	1.66	0.04	0.03
23 June	Stag	Drifter	27	27.4	0.20	0.96	0.85	0.02	0.07
23 June	Stag	Resident	15	28.3	0.20	0.86	1.30	0.04	0.10
26 June	Stag	Drifter	21	27.6	0.20	0.95	1.33	0.04	0.10
26 June	Stag	Resident	20	28.2	0.21	0.95	1.22	0.03	0.09
29 June	Stag	Drifter	8	27.7	0.20	0.95	1.87	0.05	0.07
29 June	Stag	Resident	20	28.9	0.24	0.95	1.83	0.07	0.11
28 June	Western	Drifter	7	29.8	0.27	1.02	1.15	0.05	0.12
28 June	Western	Resident	7	29.8	0.26	1.00	0.74	0.03	0.08
5 July	Western	Drifter	27	31.0	0.29	0.96	1.88	0.08	0.12
5 July	Western	Resident	20	32.1	0.35	1.04	2.39	0.08	0.08
8 July	Western	Drifter	22	31.0	0.29	0.94	3.46	0.12	0.20
8 July	Western	Resident	20	33.3	0.38	1.02	2.27	0.08	0.09
12 July	Western	Drifter	27	30.4	0.28	0.97	2.28	0.09	0.13
12 July	Western	Resident	20	32.9	0.38	1.05	2.75	0.10	0.08

Using ANOVA on calculated condition factors, a weak significant difference appeared in Western Brook, with resident salmon fry having higher condition factors (df = 1, $F = 4.119$, $P = 0.044$) compared with drifting fry (Table 2; Fig. 4). However, a more robust test such as analysis of covariance, comparing the slopes and intercepts of the weight–length relationship for the populations involved, showed that there was no significant difference between the two groups ($F = 2.424$, df = 1, $P > 0.05$), and this for all of the sampling periods ($P > 0.05$). In Stag Brook, using both statistical approaches, there was no significant difference in condition factor between the two groups of fish ($P > 0.05$). Condition factor in Stag Brook was initially higher for resident fry during the first two sampling periods. The condition of residents then declined to become lower than the condition factor of drifters on 23 June, increasing thereafter to become approximately the same values for both groups of fish for the last two sampling periods. This decrease in condition status is linked to the 22.1% weight decrease for resident fry on this particular date (Fig. 4). During the same period, a change in fry drift was observed that corresponds to the transition between the two waves of downstream movement (Fig. 2). The daily number of drifting fry in Stag Brook decreased from 247 fry (15 June) to 96 (18 June) and then up to 360 fry (24 June). It

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Fig. 4. Comparison between drifting (broken lines) and resident (solid lines) Atlantic salmon fry for mean length, mean weight, and mean condition factor sampled during the summer of 1999: (*a*) Western Brook and (*b*) Stag Brook. Standard deviation bars are indicated for each mean value.

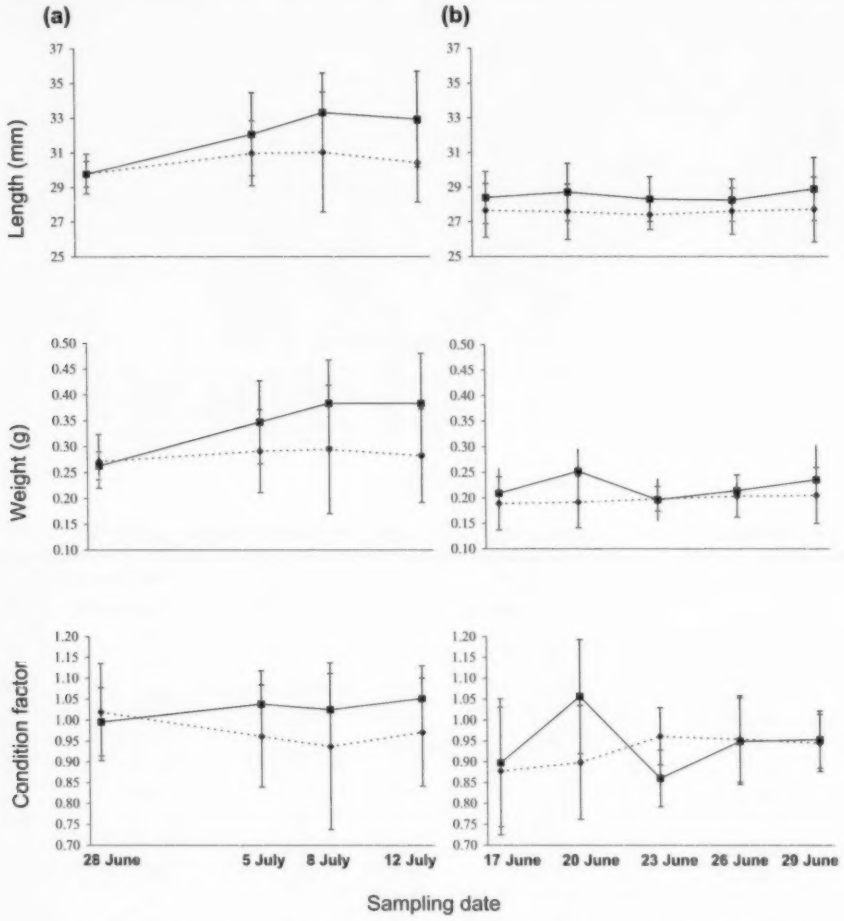
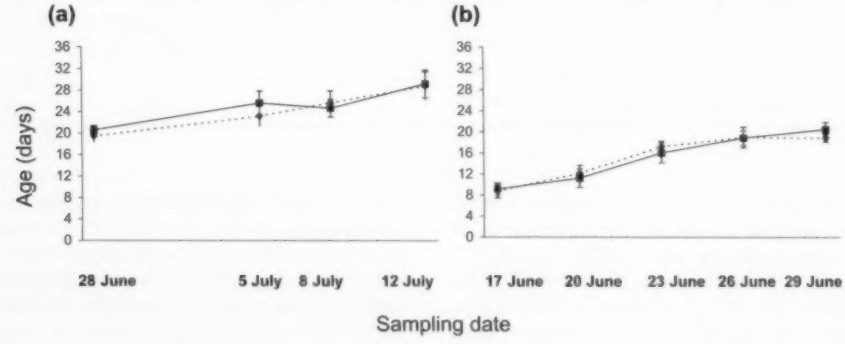


Fig. 5. Comparison between drifting (broken lines) and resident (solid lines) Atlantic salmon fry for age since emergence sampled during the summer of 1999: (*a*) Western Brook and (*b*) Stag Brook. Standard deviation bars are indicated for each mean value.



was also observed that between 15 June and 24 June 1999, water temperature dropped from 17.6 to 12.6 °C before increasing to 17.7 °C (Fig. 2) and that water level varied, with an increase of 10 cm on 16 June (Fig. 3).

Age

A comparison of age in days since emergence of drifting and resident fry indicated no significant difference between the two groups for both Western Brook (F = 3.072, df = 1,

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Fig. 6. Picture of an Atlantic salmon fry otolith and the "check ring" left at first feeding coinciding with emergence.

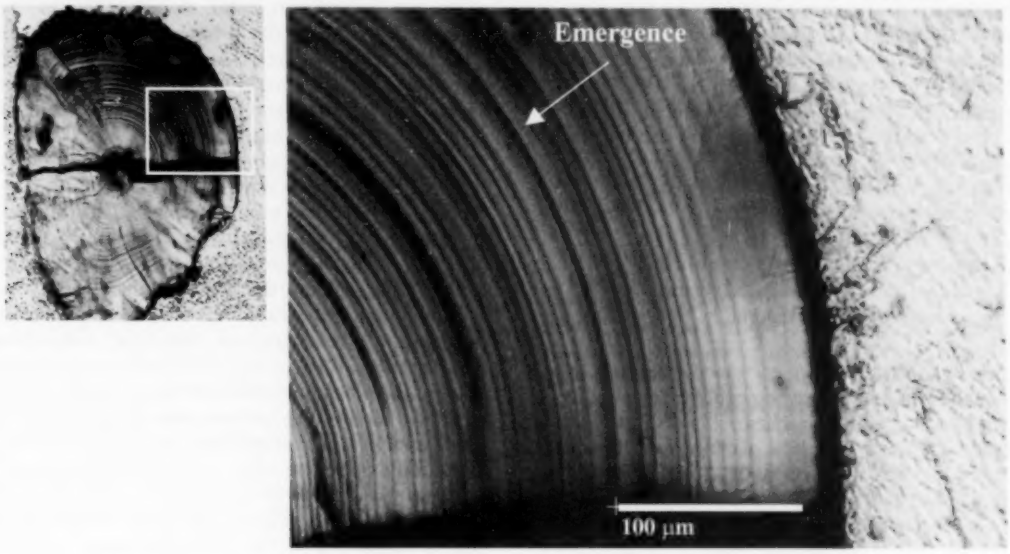
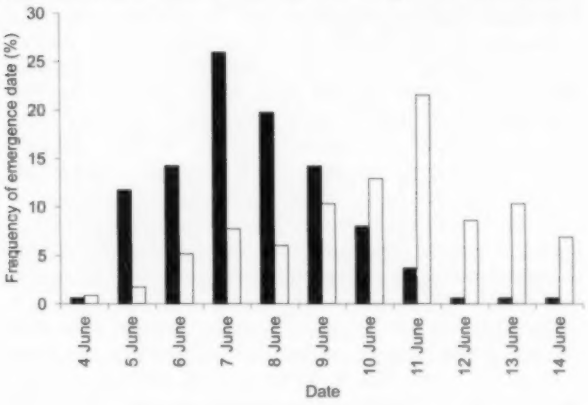


Fig. 7. Frequency of Atlantic salmon fry emerging on different days in June 1999 in Western Brook (open bars) and Stag Brook (solid bars) as estimated from otolith readings of individual fry.



$P = 0.0824$) and Stag Brook ($F = 0.820$, df = 1, $P = 0.365$) (Fig. 5). There was also no significant interaction effect between the two factors used in the analysis (group and period).

No yolk sacs were observed on sampled fish. This was expected because the youngest fish captured was estimated to be 7 days after emergence and yolk sac resorption and emergence are typically coincident in Atlantic salmon fry (Dill 1977; Northcote 1978).

During the period of fry drift in Stag Brook, the age of resident and drifting salmon fry was estimated at 7–20 days after emergence. In Western Brook, during the movement period, both groups of fish were estimated to be 19–28 days after emergence (Fig. 5). In fact, the age of the first drifting fry collected in Western Brook was similar to the age of the last fry captured in Stag Brook.

By examining the date at which the emergence "check ring" was left on the otoliths (Fig. 6), it appeared that salmon fry from Stag Brook emerged significantly earlier than salmon fry from Western Brook (one-way ANOVA, df = 1, $F = 220.6$, $P < 0.0001$). In 1999, the most frequent emergence date for salmon fry in Stag Brook was 7 June with more than 25% emerging this day, whereas 11 June was the most frequent emergence date in Western Brook when over 21% of fry emerged (Fig. 7). Therefore, although emergence started on 4 June in both streams, the emergence period was more constricted in time in Stag Brook compared with Western Brook, as was the case for drift. This is probably also related to water temperature, which increased more rapidly in Stag Brook than in Western Brook (Fig. 2).

In examining the otoliths, it seems that sampling was generally done on the same population, not on new recruits, at least in Stag Brook. In Western Brook, the first drifting fry were the earliest emergents, approximately the same date of emergence as fry from Stag Brook, but the resident fry in July were fish that emerged later (11 June and later). However, fry grew older over time and the age difference in days from the beginning of sampling to the end was correlated with the length of the sampling period in both brooks (Stag Brook: 0.91, $P < 0.0001$; Western Brook: 0.76, $P < 0.0001$).

Discussion

Our main finding was that drifting Atlantic salmon fry were significantly shorter and weighed less than resident fry. These results were consistent in two Newfoundland streams, despite the differences in water temperature regimes. However, multiple comparison tests indicated that this difference was observed mainly during July, in Western Brook, compared with Stag Brook. Our results contradict those of Ottaway and Clarke (1981) who found, during laboratory experiments, that salmon fry readily drifting downstream (drifters) were of larger than average size, but they corroborate the results of Johnston (1997) who hypothesized that drifters would be expected to be smaller than fish that hold territories successfully.

Two distinct waves of fry drifting movement, as described by Marty and Beall (1989), were only observed in Stag

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Brook. In this stream, the first wave extended from 9 June until 18 June and probably consisted of young fish, since fry sampled on 17 June were 9 days old on average. This was expected because the first wave supposedly occurs immediately after emergence (Marty and Beall 1989). However, it is also possible that this peak in drifting movement in Stag Brook could have been influenced by the variation in water temperature and (or) the water level. Between 15 June and 24 June, it was observed that water temperature dropped from 17.6 to 12.6 °C before increasing to 17.7 °C. During the same period, the water level increased 10 cm on 16 June and it could have had a major impact on fry downstream movement. In Western Brook, it seems that the first wave of dispersal was missed, since the youngest drifting fry caught in this stream were 18 days old.

Even though significant differences were found in length and weight, no significant difference could be established in condition status or weight–length relationships between drifters and residents in Western Brook as well as Stag Brook. In Stag Brook, it could be explained by the decrease in resident fry average weight observed between 20 June and 23 June. Factors that could have influenced resident weight are variations in water level and water temperature, which possibly had an impact on the quantity of available food, and the change in fry behaviour between the two waves of drift movement. To address this question, many possibilities would have to be investigated. For example, resident fry could have invested more energy in habitat defence compared with drifters during the second wave, or fry may have been hiding in the substrate, thereby avoiding competition rather than exposing themselves in the open water.

According to Marty and Beall (1989) and Johnston (1997), the second period of drifting comprised later-emerging fry that were displaced by territorial intraspecific competition and forced to seek new territories downstream. No such age difference between the drifters and the resident fry was found in this study.

Approximate date of emergence was established from otolith readings. It appeared that a time lag existed between emergence periods in the two streams. The peak of salmon fry emergence in Stag Brook was significantly earlier than that in Western Brook in 1999. This difference between the two streams seems most likely related to water temperature, which was significantly warmer in Stag Brook during the spring 1999. In fact, hatching is related to the cumulative number of degree-days (Velsen 1980), but as described by Gustafson-Marjanen and Dowse (1983), who studied salmon fry in Maine, no specific threshold temperature can be used as a trigger for hatching. The pattern of drifting movement was more constricted in time in Stag Brook compared with Western Brook and is also probably related to more rapidly warming water temperature in Stag Brook. It might be possible that salmon fry in Western Brook hatch later, spend more time in the gravel before emerging, and are older when drifting downstream because of the influence of colder water in Western Brook Pond.

The origin of the size difference could not be established in this study. It is possible that, at emergence, fry are already separated into two groups of different size. It is known that family membership can influence size (Webb et al. 2001) as well as egg size, which can effect posthatch performance (Einum and Flemming 2000). Miller et al. (1988) suggested that size differences could have major repercussions on the future of these fry, since body size has long been recognized as an important variable influencing many aspects of the physiology, ecology, and behaviour of living organisms. Both dominance rank and size attained by July can be significant predictors of future development patterns (Metcalfe et al. 1989). Fish that were dominant or larger 2 months after first feeding (or both) had a greater probability of migrating earlier than those more subordinate or smaller (or both; Metcalfe et al. 1989). However, since there was no age difference between drifters and residents, this size difference may have conferred a competitive advantage wherein drifting individuals were displaced by the aggressive behaviour of resident fish that had already settled in available territories (Chapman 1962; Mason and Chapman 1965; Solomon 1982).

In the present study, experimental design could have biased the results to some extent. Sampling sites were located near the mouths of both streams. The selection of these sites was related to previous work done in 1998 that established drifting movement in these locations, but specific spawning locations were unknown in the two streams despite efforts to locate them in 1998. Such information would have been useful in determining the exact distance of drifting and if fry from different spawning locations were mixing via drift. It is also possible that drifting behaviour and (or) the size differences may have a genetic component. We also did not investigate if resident fry and drifters have a different growth pattern, and it is possible that they begin their feeding at a different date from emergence. It this study, it was assumed that they were the same. Redd location, emergence sampling using emergence traps, fry marking using dye or other methods, and genetic analysis are recommended techniques that should be considered for future research projects on this issue.

In conclusion, although emergence commenced at approximately the same time within the two streams, the drifting movement was more protracted in time in the warmer stream, Stag Brook, compared with the colder one, Western Brook. Postemergent Atlantic salmon fry clearly separated themselves into two distinct groups, as residents and drifters, according to body size during July in Western Brook. Differences were not as strong in Stag Brook. No differences between the two groups were found with respect to age in days after emergence, reinforcing the hypothesis that competition (probably for space and (or) food) is the source of this behaviour rather than prior residence effect. However, the fate, including survival rate and fitness, of resident fish compared with drifters remains unknown and such information would be beneficial to better understand life strategies of Atlantic salmon and consequently manage this species.

Acknowledgments

The authors wish to thank K. Pilgrim, R. Delong, and C. Kennedy who assisted in collecting field data. Gros Morne National Park employees, as well as C. Mullins and P. Caines, Department of Fisheries and Oceans, Newfoundland, also provided invaluable assistance. S.P. Good and N. Aubin-Horth assisted with otolith reading. Drs. D. Quiring

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and S. Flemming and Mr. G. Chaput contributed significantly in project development. Financial support came from the Ecosystem Science Fund, Gros Morne National Park, a Natural Sciences and Engineering Research Council of Canada individual research grant, and a Meighen–Molson professorship to R.A. Cunjak.

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Detecting persistent change in the habitat of salmon-bearing streams in the Pacific Northwest

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Abstract: In the northwestern United States, there is considerable interest in the recovery of Pacific salmon (*Oncorhynchus* spp.) populations listed as threatened or endangered. A critical component of any salmon recovery effort is the improvement of stream habitat that supports various life stages. Two factors in concert control our ability to detect consistent change in habitat conditions that could result from significant expenditures on habitat improvement: the magnitude of spatial and temporal variation and the design of the monitoring network. We summarize the important components of variation that affect trend detection and explain how well-designed networks of 30–50 sites monitored consistently over years can detect underlying changes of 1–2% per year in a variety of key habitat characteristics within 10–20 years, or sooner, if such trends are present. We emphasize the importance of the duration of surveys for trend detection sensitivity because the power to detect trends improves substantially with the passage of years.

Résumé : On s'intéresse beaucoup, dans le nord-ouest des États-Unis, au rétablissement des populations de saumons du Pacifique (*Oncorhynchus* spp.) considérées comme menacées ou en voie de disparition. L'amélioration des habitats des cours d'eau qui abritent les différents stades du cycle des saumons est une composante essentielle de ce rétablissement. Deux facteurs associés, soit l'importance des variations spatiales et temporelles et la planification du réseau de surveillance, déterminent la capacité de détecter les changements stables de conditions de l'habitat résultant de dépenses importantes consenties pour son amélioration. Nous présentons une synthèse des principales variations qui affectent la détection des tendances, ainsi qu'une démonstration que des réseaux bien planifiés de 30–50 sites suivis constamment au cours des ans peuvent déceler des tendances sous-jacentes de 1–2 % par année pour une variété de caractéristiques fondamentales de l'habitat sur une période de 10–20 ans ou moins, lorsque de telles tendances existent. Nous insistons sur l'importance de la durée des inventaires pour la sensibilité des détections de tendances parce que la capacité de déceler les tendances s'améliore au cours des années.

[Traduit par la Rédaction]

Introduction

The decline of wild Pacific salmon (*Oncorhynchus* spp.) in riverine–riparian ecosystems of the Pacific Northwest has led to considerable scientific, political, social, philosophical, and financial efforts to identify causes for the decline and find solutions (Huntington et al. 1996; Nehlsen 1997; Lackey 2000). The varied and complex causes of the decline tend to fall into several broad categories: freshwater and estuarine habitat degradation, commercial and recreational harvest, hydropower (dams) and water diversion from stream channels, oceanic conditions, hatcheries, and biological interactions such as predation and competition from introduced species (National Research Council 1996; Committee on Environment and Natural Resources 2000; Federal Caucus 2000). These factors affect all life stages to varying degrees and, in aggregate, affect salmonid populations at regional scales (e.g., bioregions, provinces, evolutionarily significant units) over time scales of a decade and longer. Therefore, solutions addressing the multiple causes of salmonid decline must also vary, both in spatial and temporal scales and in scientific and sociopolitical complexity (Federal Caucus 2000; Lackey 2000).

The degradation and potential recovery of freshwater riparian and stream channel habitat is an important part of salmon recovery. Human settlement along stream and river corridors during the past 150 years has altered the fundamental processes that created the habitat conditions under which salmonid populations have evolved and adapted over centuries (Bisson et al. 1992; Beechie and Bolton 1999; Naiman et al. 2000). These fundamental processes include the supply of sediment, wood, and nutrients to channels, the flow regime, connections to floodplains, and riparian vegetative cover and composition. Habitat conditions altered by human-induced changes to fundamental processes include the longitudinal frequency and depth

Received 3 February 2003. Accepted 29 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 31 March 2004.
J17320

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 doi: 10.1139/F03-157 © 2004 NRC Canada

of pools, the composition of stream bed substrate, riparian vegetative cover, the complexity of channel habitat, and floodplain connectivity.

In response to these changes, a variety of plans and approaches are being developed and implemented to improve freshwater habitat conditions thought to be most important to salmonid survival (Schmitten et al. 1995; Tuchmann et al. 1996; Independent Scientific Group 1999). Local-scale activities are underway, such as adding habitat structure to stream reaches (wood placement, streamside stabilization, native riparian vegetation planting) and modifying road building and management to minimize excessive sediment supply to streams (proper culvert construction, retiring of inactive roadbeds, construction of new roads on stable land types). Broader regional-scale principles and procedures are also being implemented, such as conducting watershed analysis to guide watershed restoration. Federal and state policies have been embodied in the Northwest Forest Plan (Tuchmann et al. 1996), in the Oregon Plan for Salmon and Watersheds (Nicholas 1997), and in the accumulation of legal decisions on lawsuits aimed at ensuring compliance with existing mandates promulgated by the Clean Water Act or the Endangered Species Act.

A key factor in determining the success of these combined activities and policies is a sound monitoring program that tracks changes over time frames appropriate to the spatial and temporal scales of expected responses. Given that habitat degradation has probably been occurring gradually for decades and longer, and that recovery activities will not restore habitat within a short time frame at regional scales, a monitoring plan that tracks habitat features at regional spatial scales over decades is of primary importance. A step toward designing and implementing such a monitoring program is to evaluate trend detection capability. What trends are we likely to detect at what cost? An issue sometimes raised is that the features of interest are so spatially and temporally variable that only the strongest of trends can be detected. As we show, however, a carefully designed monitoring network can quantify and manage spatial and temporal variation and detect gradual changes in key indicators.

During the past decade, we conducted a series of regional monitoring surveys in small, perennial streams in the size range important for spawning and rearing of Pacific salmon, measuring many significant attributes of stream and riparian habitat. The survey designs allowed us to calculate components of variation important in detecting regional trends (Urquhart et al. 1998; Larsen et al. 2001). In this article, we describe the key components of variation that affect regional trend detection, summarize our estimates of these components for several key physical habitat indicators, and demonstrate the trend detection sensitivity of a regional network of sites (its power to detect trends of specified magnitudes).

Materials and methods

Trend detection

The ability of a monitoring program to detect trends is sensitive to spatial and temporal variation in the target indicators as well as to design choices for a network of sites and the timing and frequency of sampling (Urquhart et al. 1998; Urquhart and Kincaid 1999; Larsen et al. 2001). Restoration of habitat is expected to produce conditions that vary spatially and temporally and that could mimic conditions to which salmonids have adapted (Reeves et al. 1995; Abbe and Montgomery 1996; Bisson et al. 1997). To evaluate the effects of spatial and temporal variation, we have focused on four major components of variation whose management is useful for evaluating and controlling trend detection power: site, year, interaction, and residual variation (Table 1).

We define trend as a persistent unidirectional (positive or negative) change across years, as elaborated in Urquhart et al. (1998). Trend can be with or without pattern. In either case, a trend contains an underlying linear component. Our evaluation of trend detection capability relies on the detection of this underlying linear component, which will be present with any complex, consistent pattern of change (Urquhart et al. 1998). More complex change and trend detection methods might detect trends sooner, and with greater power, than we suggest here. We do not know what the pattern will be ahead of time, but once it unfolds (if present), trend detection techniques that take the pattern into account are likely to indicate trend sooner than a simple linear approximation. Hence, our evaluation can be considered a conservative evaluation of trend detection capability (power to detect a specified trend if such a trend is present) (Gerrodette 1987; Peterman 1990; Gibbs et al. 1998). We hypothesize that the underlying linear component will be different from zero when a trend is present. Trend detection sensitivity, therefore, evaluates the likelihood of distinguishing whether a slope (change per year) of a specified magnitude in the mean value of a habitat characteristic (e.g., pool depth) across a network of streams differs from zero.

Stream surveys

We base our evaluation on six surveys that included 392 stream reaches and 200 repeat visits. These surveys were conducted in Oregon and Washington from 1993 to 1999. Most were from 1 to 3 years in duration, but one survey lasted 6 years (Table 2). These surveys targeted wadeable perennial streams occupied by diverse salmon species and life stages. A team of two persons measured a comprehensive set of habitat characteristics in about 3 h with simple measuring devices, such as tape measures, clinometers, surveying rods, and visual estimation. Stream reach length ranged from 150 m to 1 km; catchment areas ranged from 0.1 to 150 km^2 (Kaufmann and Robison 1998; Kaufmann et al. 1999).

For each survey, a region of interest was specified (e.g., the stream network in the coastal province of Oregon and Washington or the stream network in the Central Cascades of Oregon). Then, a set of stream sites (specified by the desired sample size) was selected for field monitoring from the network, as represented on 1 : 100 000-scale U.S. Geological Survey digital stream traces. The site selection procedure uses a probability survey design similar to a simple random sample, with the exception that it guarantees that any selected sample has the same spatial distribution as the stream spatial distribution (Stevens and Olsen 1999). Because of the randomized selection process, measurements made at the sampled locations can be used to infer conditions within the entire specified network of interest. Each design was constructed to facilitate estimation of the applicable components of variation (specified in Table 1). Field crews sampled the

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Table 1. Summary of the four components of variation important for evaluating regional trend detection power (Urquhart et al. 1998; Larsen et al. 2001).

Component of variation	Description
Site	Persistent differences among stream reaches across a region are expressed through site-to-site variation. For example, stream size or gradient differs across the landscape. Some stream channels are constrained by V-shaped valleys and are regularly scoured to bedrock; other channels are contained in broad alluvial valleys and have high alluvial loads. Similarly, some stream channels are inherently more capable of supporting more deep pools than others, or more large wood. These differences among stream reaches in a region are captured by site-to-site variation
Year	The synchronous or coherent yearly variation among all sites in a network that might be influenced by regional-scale forces such as climate, broad-scale disturbances, or ocean conditions. An example is the synchronous variation in stream flows that are higher than normal at all sites during a wet year but lower than normal at all sites during a dry year
Interaction	The independent, desynchronized yearly variation among all sites in a network, subject to local-scale influences. An example is the yearly variation in the amount of wood or fine sediments in stream channels. The supply of wood or sediments might be quite patchy spatially and variable temporally such that some reaches receive high amounts in particular years but lower amounts in other years, whereas the reverse might be true for other reaches
Residual	Residual variance captures the remaining variation. It consists primarily of the short-term variation during the temporal window when measurements are made, measurement error, and team-to-team differences in applying the same field protocol

Table 2. Summary of the regional surveys on which the variance analyses are based.

Region	No. of sites	No. of within-year revisits	No. of between-year revisits	Years covered by survey
Willamette Valley/Cascades (Oregon)	46	22	51	1993–1997
Oregon–Washington Coastal Ecoregion	139	35	59	1994–1996
Upper Deschutes (Oregon)	54	12	1	1997–1998
Upper Chehalis (Washington)	27	5	0	1997
Tillamook/Kilchis (Oregon)	53	6	1	1998–1999
Oregon Coastal Ecoregion	73	8	0	1998
Total	392	88	112	1993–1999

selected stream sites during a low-flow summer index window, generally between July and mid-September.

Habitat attributes

This evaluation focuses on several habitat characteristics (*i*) commonly agreed upon as important to salmon and other aquatic species, (*ii*) frequently targeted in restoration activities, and (*iii*) expected to respond to improved management practices (MacDonald et al. 1991; Committee on Environment and Natural Resources 2000; Bauer and Ralph 2001). Although numerous other stream channel features are important to salmon and are often incorporated into monitoring programs, we chose these as illustrative of patterns of variation and of the potential for detecting subtle, decadal-scale trends. Our selection of habitat attributes does not imply that salmon abundances would necessarily increase, should positive trends be present. The approach is applicable to other streams in other regions. Our selected habitat characteristics include pools, riparian canopy cover, fine sediments, and large wood.

Pools

Pools are quiet waters of greater than average stream depth distributed along the longitudinal profile of a stream channel. Pools serve a variety of functions for many salmon species and life stages, particularly for juveniles (Beechie and Sibley 1997; McIntosh et al. 2000). It is thought that both the frequency of pools (e.g., number of pools per unit length of stream channel) and the average pool depth have decreased over the past century as a result of broad-scale human activities (Beechie and Sibley 1997; McIntosh et al. 2000; Collins et al. 2002). Regional increases in average pool depth and pool frequency are expected as a response to numerous local- and regional-scale management actions. Our surveys estimate residual depth (Lisle 1987; Robison and Kaufmann 1994; Wood-Smith and Buffington 1996), defined as the depth of water that would remain if stream flow ceased; this measure of pools removes the effect of discharge variation on the definition and characterization of pools.

Riparian canopy cover

Shading of sunlight by the riparian canopy cover maintains the cool stream temperatures necessary for salmon reproduction and growth (Rutherford et al. 1997; Mitchell 1999; Bartholow 2000). Riparian cover also serves as a source of small and large (especially large wood) particulate organic matter, which is important to the maintenance of channel structural complexity and metabolism (Gregory et al. 1991; Naiman et al. 2000).

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Streamside activities, such as farming, silviculture, and construction, are responsible for substantial reduction in riparian canopy cover. We measure riparian cover as the proportion of a convex hemispherical densiometer on which the reflection of riparian vegetation is visible (Kaufmann and Robison 1998; Kaufmann et al. 1999).

Fine sediment

An excess of fine sediment (sediment particles of <2 mm) in stream channels fills spaces in larger sized substrates, thereby eliminating critical habitat and reducing the flow of oxygen to invertebrates and to developing salmon eggs and juveniles (Kondolf 2000). Much current management activity attempts to reduce or eliminate excess fine sediment in stream channels through proper road construction and maintenance as well as prevention of timber harvest in riparian areas or on slopes particularly sensitive to mass wasting. By means of systematic pebble count procedures (Wolman 1954), we measure fine sediment as the proportion of sand, silt, and finer substrate particles estimated to be <2 mm in diameter (Kaufmann and Robison 1998; Kaufmann et al. 1999).

Large wood

Research during the past 20 years has revealed the ecological importance of large wood (generally defined as pieces >10 cm in diameter and 1.5 m long) in stream channels. It creates pools and cover for aquatic organisms, stabilizes stream banks, and fosters habitat diversity (Harmon et al. 1986; Maser and Sedell 1994; Ralph et al. 1994). Until the 1970s, stream channels were actively cleared of large wood. As a result of subsequent research, management activities now encourage the replenishment of wood in stream channels through a variety of actions. Wood is placed directly into stream channels, the removal of large wood is prevented, and riparian corridors are protected to promote the regrowth of natural riparian vegetation that regenerates natural supplies of wood to channels. However, stream cleaning is still widespread in urban and agricultural settings. Our protocols count the number and sizes of pieces of large wood and express results in terms of the volume of wood per unit length of channel (Kaufmann and Robison 1998; Kaufmann et al. 1999).

Analytical methods

For each of the four habitat characteristics, we estimated the magnitude of the components of variation for each survey separately; we also made estimates from all surveys combined. We use a linear model of the following form as a framework for identifying and calculating the components of variation (Table 1): $X_{ijk} = \mu + \mathrm{St}_i + Y_j + \mathrm{St}Y_{ij} + R_{ijk}$, where X_{ijk} is the response for the kth visit at stream site i during year j, μ is the overall mean, St_i is the random effect due to stream site i, Y_j is the random effect due to year j, $\mathrm{St}Y_{ij}$ is the random effect due to the interaction of stream site i and year j, and R_{ijk} is the random effect due to residual variation for the kth visit at stream site i during year j. In this model, subscript i ranges from 1 to l (the number of stream sites surveyed), subscript j ranges from 1 to t (the number of years of data), and subscript k ranges from 1 to r_{ij} (the number of visits during year j at stream site i). The components of variation are defined as follows: $\mathrm{Var}(\mathrm{St}_i) = \sigma^2_{\mathrm{Stream}}$ for all i, $\mathrm{Var}(Y_j) = \sigma^2_{\mathrm{Year}}$ for all j, $\mathrm{Var}(\mathrm{St}Y_{ij}) = \sigma^2_{\mathrm{Interaction}}$ for all i and j, and $\mathrm{Var}(R_{ijk}) = \sigma^2_{\mathrm{Residual}}$ for all i, j, and k. Total variance then consists of the sum of the four components: site variance ($\sigma^2_{\mathrm{Stream}}$), year variance ($\sigma^2_{\mathrm{Year}}$), interaction variance ($\sigma^2_{\mathrm{Interaction}}$), and residual variance ($\sigma^2_{\mathrm{Residual}}$).

In multiple-site surveys, in which a network of sites is monitored consistently over time, the components of variation are captured by the attribute's time series. If the surveys are properly designed, the data obtained from multiyear monitoring can be used to estimate the magnitude of each of these components of variation. The sum of squares in an analysis of variance model can be partitioned into each of the components of variation and converted to mean squares. Mean squares and sample allocation are used to estimate variances as follows:

$$s^2_{\mathrm{Total}} = s^2_{\mathrm{Stream}} + s^2_{\mathrm{Year}} + s^2_{\mathrm{Interaction}} + s^2_{\mathrm{Residual}}$$

$$s^2_{\mathrm{Residual}} = \mathrm{MS}_{\mathrm{Residual}}$$

$$s^2_{\mathrm{Stream}} = (\mathrm{MS}_{\mathrm{Stream}} - \mathrm{MS}_{\mathrm{Interaction}}) / N_{\mathrm{Year}} N_{\mathrm{Visit}}$$

$$s^2_{\mathrm{Year}} = (\mathrm{MS}_{\mathrm{Year}} - \mathrm{MS}_{\mathrm{Interaction}}) / N_{\mathrm{Stream}} N_{\mathrm{Visit}}$$

$$s^2_{\mathrm{Interaction}} = (\mathrm{MS}_{\mathrm{Interaction}} - \mathrm{MS}_{\mathrm{Residual}}) / N_{\mathrm{Visit}}$$

The estimated components of variation (s^2) and mean squares (MS) are descriptively subscripted. Sample sizes (N) are subscripted by number of stream sites, years, and visits to a stream within a year. These formulas assume a balanced design in a sites-by-years matrix, with revisits to all sites each year. Most standard statistical software packages provide routines for calculating the components of variation when balanced designs are used; sometimes these are called repeated measures designs. For unbalanced designs (in which not all sites are revisited within a year nor are all sites monitored each year), the same framework is used for estimating components of variation, but the calculations are more complicated. An alternative approach for estimating components of variation for unbalanced designs is to use estimation methodology based on maximum likelihood, which is available in many statistical programs (e.g., SAS and S-PLUS). Specifically, a variant of maximum likelihood estimation referenced as restricted maximum likelihood can produce components of variation estimates for any design.

Our evaluation of trend detection capability considers regional trend as the average across a set of site-specific trends. Consider a network of stream sites that has been monitored for years. At each stream site, the temporal trajectory across years can be evaluated for site-specific trend. The average value of this set of site-specific trends comprises regional trend. As noted earlier, any trend, patterned or not, has an underlying linear trend; it is this underlying linear component of the consistent trend that we hypothesize to be different from zero and on which we base trend detection capability. Trend detection sensitivity, therefore, evaluates whether the slope differs from zero and is based on an expansion of the usual linear regression model (e.g., Draper and Smith 1967; Urquhart et al. 1998; Larsen et al. 2001) as follows:

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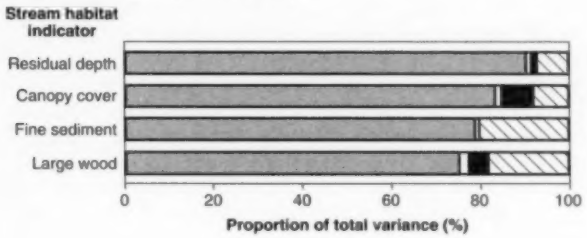
Fig. 1. Relative magnitude of the four components of variance for the key habitat attributes evaluated illustrating the dominance of the site component of variation and the relatively small magnitude of both the year and interaction components. Components of variation: site (shaded bars), year (open bars), interaction (solid bars), and residual (hatched bars).



$$(1)\qquad \mathrm{var(slope)} = \frac{\dfrac{\sigma^2_{\mathrm{Stream}}}{N_{\mathrm{Stream}}} + \sigma^2_{\mathrm{Year}} + \dfrac{\sigma^2_{\mathrm{Interaction}} + \dfrac{\sigma^2_{\mathrm{Residual}}}{N_{\mathrm{Visit}}}}{N_{\mathrm{Stream}}}}{\sum (Y_t - \bar{Y})^2}$$

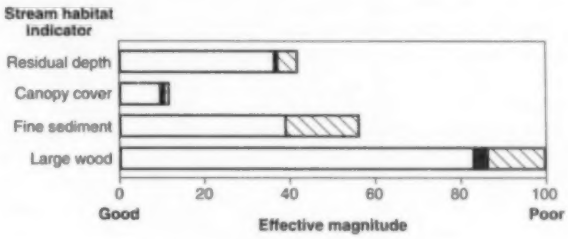
where σ^2 refers to variances as subscripted, N refers to the number of stream sites or the number of visits to stream sites in a particular year, and Y refers to years. Urquhart et al. (1998) provided the formal statistical basis for the trend detection model and power estimation that incorporates var(slope) along with justification for assumptions of approximate normality regarding the distribution of slope values. Exact computations of power depend on normality, but the comparative patterns that we describe hold up in the absence of normality.

The numerator of eq. 1 contains the components of variation described (Table 1) and illustrates how various design choices can affect trend detection capability; the denominator corresponds to the *x*-axis of a standard linear regression and is expressed in years because of the expected long time frame likely to be needed for trends in stream habitat to appear. In the numerator, the effect of the stream component of variance vanishes if revisits to stream sites are incorporated into the design. The interaction and residual variances are controlled by the number of sites in a network, but year variance is not. Furthermore, residual variance is controlled both by number of sites in the network and by number of revisits to sites within a year, but interaction variance is controlled only by the number of sites in the network. The effect of all components of variance on the ability to detect trends (var(slope)) is controlled by the duration (denominator) over which the survey network in monitored.

Results and discussion

Individual variance estimates from each survey did not differ in any substantial way from the grand estimation. The results summarize the relative magnitude of each of the four components, scaled to 100 so that comparisons can easily be made across habitat attributes measured on different scales and with different measurement units (Fig. 1). As might be expected because of the range of stream types, sizes, and local settings, most of the variation is associated with site-to-site differences among the streams. If unaccounted for in survey designs intended to detect regional trends, this site component of variation can substantially diminish sensitivity (Urquhart et al. 1998). However, if patterned revisits are incorporated across years, the effect of site-to-site differences is effectively eliminated in a manner analogous to experimental designs that use self-pairing.

Fig. 2. The equation for the variance of a slope (eq. 1) can be viewed as a sum of three parts when stream sites are revisited across years: year, interaction, and residual. The relative effect of these parts on the variance of a slope is illustrated as a bar graph, rescaled to 100% for the most variable slope, for a design in which 50 stream sites are visited once annually. The effects of the interaction and residual components are minor compared with the dominant effect of the year component. Components of variation: year (open bars), interaction (solid bars), and residual (hatched bars).



The remaining components of variation affect sensitivity to trends to varying degrees, depending on design choices (Urquhart et al. 1998; Urquhart and Kincaid 1999; Larsen et al. 2001). The effect of the residual component of variation is sensitive to number of revisits to a site within a year (or within the seasonal temporal window during which the survey is conducted), but the effect of the interaction component is not. Both, however, are affected by the number of sites in the survey. As a result, it is generally better to add sites to a survey rather than revisit sites within the year, unless revisits to sites are much less costly than visits to new sites. The final component of variation, the year effect, cannot be managed by the same design choices as the other three components; regional trend detection is particularly sensitive to its magnitude (Urquhart et al. 1998; Urquhart and Kincaid 1999; Larsen et al. 2001). Rather, it is managed through measurement or evaluation of the factors controlling it (e.g., oceanic conditions, decadal weather patterns, regionally consistent stream flow patterns). If these controlling factors are identified and their effects on target variables quantified by modeling, then the "year effect" can be reduced.

To illustrate the interactions of these components and their effects on trend detection sensitivity, we examined their influences on detection of a 1–2% per year trend with a network of 50 sites. With a set of 50 sites visited every year, the effects of the interaction and residual components become minimal compared with the now undiminished year effect, whose relative influence is magnified (Fig. 2). When the year effect is substantial, increasing the number of sites in a network has little effect on trend detection.

Using the power of a statistical test to detect an outcome is increasingly being accepted as a means of evaluating sensitivity (Peterman 1990; Gibbs et al. 1998; Fox 2001). Power

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Fig. 3. Power to detect 1% per year (broken lines) and 2% per year (solid lines) trends, with 80% power for each indicator, in the four habitat indicators (●, canopy cover; ▲, residual depth; no symbols, fine sediment; ■, large wood) with a monitoring network of 50 sites visited annually ($\alpha = 0.05$).

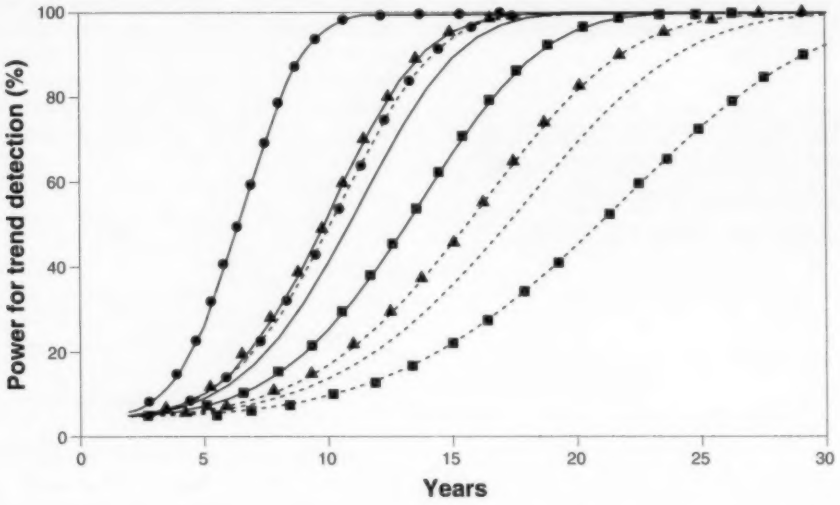

Table 3. Number of years to detect 1% per year and 2% per year trends in habitat attributes with 80% likelihood, if specified trends occur, as a function of number of monitoring sites sampled annually ($\alpha = 0.05$). For comparison, sensitivity (in parentheses) is estimated for a design that uses a random set of sites monitored each year.

No. of sites	Residual depth	Canopy cover	Fine sediment	Large wood
1% per year				
10	22 (40)	15 (24)	28 (43)	32 (44)
20	21 (33)	14 (20)	24 (35)	29 (37)
30	20 (30)	14 (18)	23 (32)	28 (34)
40	20 (28)	13 (17)	22 (29)	27 (32)
50	20 (26)	13 (16)	21 (28)	27 (31)
2% per year				
10	14 (25)	10 (15)	18 (27)	20 (28)
20	13 (21)	9 (13)	15 (22)	18 (23)
30	13 (19)	9 (11)	14 (20)	17 (21)
40	13 (17)	8 (11)	14 (19)	17 (20)
50	12 (17)	8 (10)	13 (18)	17 (20)

describes the likelihood of detecting an outcome if that outcome occurs. For example, how likely are we to detect a 1–2% per year trend in our selected physical habitat characteristics, if such a trend occurs, as a function of the duration of a survey? A 1–2% per year trend is a rather small trend, amounting to a proportional change of about 15–30% of the initial value in 15 years. If trends of this magnitude indeed occur in these habitat attributes, the likelihood of detecting them is high within 10–20 years (80% and higher detection probability, 5% probability of incorrectly asserting a trend; Fig. 3). Power is clearly sensitive to the duration of the survey; a few additional years of monitoring increases sensitivity substantially, as shown by the steepness of the power curves.

Trend detection, based on these estimates of the variance components, is relatively insensitive to the number of sites in the survey (Table 3). We varied the number of sites from 10 to 50 and found, for some of the indicators, relatively little difference in the number of years to detect 1% and 2% per year trends. However, because surveys of this nature are intended to represent conditions at a regional scale, we suggest that at least 30–50 sites be used. Fewer sites might yield unacceptably high uncertainty for regional estimation. These results indicate a fairly consistent time frame within which subtle trends in stream habitat characteristics, if present, would be detectable. This consistency should be useful as a guide for communicating expectations for detecting underlying regional changes in the habitat of northwest streams in response to the array of current and potential management actions.

For contrast, we also illustrate trend detection sensitivity for less well designed surveys. For example, if the survey did not revisit sites across years, as in a design in which sites were selected at random each year, the site component of variation (divided by the number of sites in the survey) would be included as part of the numerator of eq. 1. The site component of variation is much larger than the sum of interaction and residual, accounting for 80–90% of the total variation (Fig. 1). The magnitude of site variance far outweighs the variation in interaction and residual variation among the various individual surveys. Hence, a survey design that includes random selection of sites each year can be considered a "worst-case" scenario for these indicators. With such worst-case designs, trend detection sensitivity could be substantially lower, particularly if relatively few sites are monitored, than in cases with sites revisited annually (as contrasted in Table 3). However, achieving the specified power for trend detection for some indicators is delayed only a few years, especially if 30–50 sites are used in the survey.

Although we use 50 sites per year, visited annually, to illustrate trend detection sensitivity, nearly the same power

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can be achieved in a 10- to 20-year time frame with designs that use different patterns of visits to sites. Designs that incorporate a cyclical pattern of revisits to sites across years can be nearly as powerful as an annual design after three cycles (Urquhart et al. 1998; Urquhart and Kincaid 1999). For example, in a 4-year panel design, a different set of 50 sites would be monitored each year for 4 years. Then in year 5, the first year's sites would be revisited; in year 6, the second year's sites would be revisited, and so on. Adding some revisits within years and between adjacent years would allow estimation of the components of variation. An ongoing evaluation of variation would allow the design to be adjusted if the observed magnitude of the components of variation differed from that expected. Although panel designs are somewhat less sensitive to trend detection than annual visits, they have the advantage of visits to a larger number of different sites for essentially the same cost. The larger sample size greatly increases the utility of the network for assessing status and regional patterns and can allow for finer resolution in evaluating separate classes of streams. Survey designs that include visits on alternate years do not hamper trend detection sensitivity significantly; they only delay trend detection by a few years. Crucial to the success of various designs, however, is continuance of a consistent monitoring program over years. Trend detection capability increases dramatically with time. The actual details of the temporal design do not matter as much as a commitment to the long-term integrity of the survey.

Survey designs of the type implied here are also flexible with respect to the resource of interest. Our results cover a rather broad geographic range of streams across Oregon and Washington. Nevertheless, they suggest that subtle trends in habitat condition might be detectable. We do not mean to imply that a monitoring network of 30–50 sites across the Northwest can adequately address all of the many questions about changes in habitat condition in streams. However, research could focus on specific geographic subpopulations of streams, specific stream channel types within them (e.g., Montgomery 1999), or specific types of management actions. There might be interest in small headwater coastal streams in which wood and sediment recruitment would be expected to be high. Trends might be more visible for these attributes there. Similarly, particular channel types, such as low-gradient, "response" channels, might be expected to be more responsive to management actions than other channel types (Montgomery and MacDonald 2002). The surveys can be designed to monitor networks of sites within the channel type of interest. It is encouraging that fairly small trends should be detectable in reasonably short time frames.

Given the broad agreement on the importance of several key stream habitat features, the huge expenditures allocated to salmon restoration (U.S. General Accounting Office 2002), and the 10- to 20-year time frame over which subtle trends are likely to be detected, it seems wise to begin monitoring programs that focus, at a minimum, on a core set of habitat elements, recognizing that complete agreement on the exact set, and the field procedures for their measurement, is unlikely. An adaptive monitoring perspective could be adopted (Ringold et al. 1999) to allow for estimation of the important components of spatial and temporal variation and use of that information to refine the designs through an iterative process without losing the value of the data already collected. Compared with expenditures on various aspects of habitat restoration and protection, costs of monitoring are relatively minor. Furthermore, the cost effectiveness of monitoring programs can be greatly enhanced by initiating them soon, thereby capitalizing on the substantial effect that survey duration has on the ability to detect trends.

Acknowledgments

We acknowledge the support of numerous individuals involved in data collection and processing, the review comments of S. Katz, C. Jordan, and S. Ralph and S. Christie's and S. Pierson's editorial and graphics support, respectively. The information in this document has been funded by the U.S. Environmental Protection Agency in part through Cooperative Agreements CR 824682 with Oregon State University (N.S.U.) and CR 829095 with Colorado State University (N.S.U.) and contract No. 68-D-01-005 to Dynamac International (T.M.K.). This manuscript has been subject to review by the National Health and Environmental Effects Research Laboratory, U.S. Environmental Protection Agency, and approved for publication. Approval does not signify that the contents reflect the views of the Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

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An integrated model for growth incorporating tag–recapture, length–frequency, and direct aging data

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Abstract: A maximum likelihood method for modelling fish growth is presented that integrates data from three key sources of growth information: tag–recapture studies, length–frequency samples from commercial catches, and direct aging data from hard-parts analyses. Previous studies have almost exclusively modelled growth using only one of these sources of information. Different data sources are often most informative about different portions of the life cycle. The development of an integrated approach allows for the different data sources to complement each other and provide more comprehensive and robust estimates of growth parameters. The integrated method is applied to data sets from southern bluefin tuna (*Thunnus maccoyii*) using the von Bertalanffy growth curve as well as a more sophisticated growth curve that makes a smooth transition between two von Bertalanffy curves with different growth rate parameters. The latter is found to provide a significantly better fit and supports previous findings that southern bluefin tuna experience a transition in growth during the juvenile stage of life. Many species exhibit a seasonal growth pattern, including southern bluefin tuna for which growth is fastest during the austral summer. A method for incorporating an annual seasonal component into the analysis is described and applied.

Résumé : Nous présentons une méthode de vraisemblance maximale pour la modélisation de la croissance des poissons qui intègre les données provenant de trois sources importantes de renseignements sur la croissance, soit les études de marquage–recapture, les échantillons de longueurs–fréquences provenant des pêches commerciales et les données de détermination directe de l'âge par l'analyse des structures anatomiques dures. La plupart des études antérieures ont modélisé la croissance presque exclusivement à partir d'une seule de ces sources. Les sources différentes de données apportent souvent des informations sur des phases différentes du cycle biologique. La mise au point d'une approche intégrée permet aux différentes sources de renseignements de se compléter les unes les autres et de fournir des estimations plus complètes et plus robustes des paramètres de la croissance. Nous appliquons notre méthode intégrée à des séries de données sur le thon rouge du Sud (*Thunnus maccoyii*) à l'aide de la courbe de croissance de von Bertalanffy, mais aussi d'une courbe plus complexe qui opère une transition harmonieuse entre deux courbes de von Bertalanffy qui ont des paramètres de croissance différents. Cette dernière courbe permet un ajustement significativement meilleur et appuie les observations antérieures selon lesquelles la croissance du thon rouge du Sud passe par une phase de transition durant le stade juvénile du cycle biologique. Plusieurs espèces possèdent des patterns de croissance saisonniers, y compris le thon rouge du Sud chez qui la croissance est plus rapide durant l'été austral. Nous décrivons une méthode pour incorporer une composante saisonnière annuelle à l'analyse et nous l'appliquons aux données.

[Traduit par la Rédaction]

Introduction

The growth of a fish is a fundamental component of fisheries research. Growth models are used either directly or indirectly in stock assessments to estimate the age composition of the catch, plus changes in growth have important implications about stock status. Information for studying fish growth can be obtained from a number of sources. Probably the three most common are (*i*) fish length and time at liberty data from tag–recapture experiments, (*ii*) length–frequency data from commercial catches or research surveys, and (*iii*) direct age and length data with age estimated from annual deposits in hard tissue such as otoliths, scales, or vertebrae.

Various methods for fitting growth models to any one of these data sources individually have been developed. For tag–recapture data, the age of a fish at release is unknown, so the traditional approach has been to model the incremental change in length of the fish over the time that it was at liberty (Fabens 1965; Francis 1988*b*; James 1991). More recently, maximum likelihood approaches have been developed that model the joint density of the release and recapture lengths as opposed to modelling the length increment (Palmer et al. 1991; Wang et al. 1995; Laslett et al. 2002). In these cases, the age at release is modelled as a random variable.

For species with a peak spawning period, the length–frequency distribution of fish caught over a limited time interval will ordinarily exhibit modes corresponding to different

Received 11 December 2002. Accepted 30 November 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 31 March 2004.
J17240

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 doi: 10.1139/F03-163 © 2004 NRC Canada

age classes, at least for younger ages. The progression in length of these modes over time can be tracked to give an estimate of growth. In particular, seasonal growth patterns can often be identified. Methods have been developed to analytically separate the modes by assuming that the distribution is a finite mixture of normal or lognormal distributions (Hasselblad 1966; Macdonald and Pitcher 1979). Approaches that incorporate the estimation of a parametric growth curve into the length–frequency analysis have also been developed (Schnute and Fournier 1980; Fournier et al. 1990; Leigh and Hearn 2000).

Direct age data are a useful source of growth information for species that deposit annual growth rings in their scales, otoliths, vertebrae, or other hard tissue. The ability to determine age by counting the number of growth bands has been validated for many species, including southern bluefin tuna (SBT) (*Thunnus maccoyii*) (Clear et al. 2000). The best tissue and technique to use depends on the species and the specimen, and successful aging methods have not been found for many species. Direct age and length information has been used to estimate growth parameters in numerous studies, including those on tunas (Thorogood 1987; Gunn and Farley 1998; Alves et al. 2002).

Although many studies exist that estimate growth using one of the above data sources, analyses that integrate multiple data sources have been much rarer. Some papers have compared estimates of growth obtained from different data sources (Labelle et al. 1993). Others have used one data source to supplement another, such as Hearn and Polacheck (2003) who used the mean length of age-1 SBT from length–frequency data to convert the length–time relationship estimated from tag–recapture data to a length–age relationship. Although these studies make use of more than one data source, they do not attempt to model the data jointly. An exception is Kirkwood (1983), who estimated growth parameters for SBT using a joint analysis of length increment data from tagging studies and age at length data determined from a crude modal analysis of length–frequency distributions. We know of no analysis that integrates all three data sources into a unified growth model.

Different data sources will often be most informative about different portions of the life cycle and different aspects of growth. For example, tag–recapture data are the only data that provide more than one observation per fish and, thus, valuable information about how individuals grow. Length–frequency data collected from the commercial catches are usually more abundant and more consistent over time than data from scientific research programs and are useful in revealing seasonal patterns in growth; however, they are only informative about young ages. Direct aging data are, as the name suggests, the only data with a direct estimate of the age of individuals, and they often provide the only information on older individuals. The development of an integrated approach would allow for the different data sources to complement each other and provide a more robust and comprehensive basis for modelling growth.

In this paper, we present a maximum likelihood approach for modelling growth that incorporates a likelihood component for each of tag–recapture data, length–frequency data, and direct age–length data. Questions have been raised about the validity of estimating mutual growth parameters using more than one data source (Francis 1988*a*). This issue arises when tag–recapture data are modelled using length increments and times at liberty because growth is then being modelled as a function of size (at tagging) rather than age. The controversy lies in whether the growth parameters in a size-based tag–recapture model have the same interpretation as they do in age-based models used for the other data sources. In our approach, we model the release and recapture lengths from tag–recapture data as a function of age by treating age at tagging as a random variable, and therefore, this issue becomes irrelevant.

Our method was developed and will be illustrated in the context of SBT. However, it should be broadly applicable to other species for which similar data are available. SBT is an important species to both Australian and Japanese fisheries, and hence, its growth has been intensely studied. Nevertheless, previous growth models are not fully satisfactory in that they have been estimated using only one source of data, and the data from any one source do not provide complete information about SBT growth over their life span (refer to SBT data section later in this paper).

We begin by describing the integrated model and estimation method. A statistical model (in terms of a generic growth curve) is described for each data set separately, along with a corresponding likelihood function. The overall objective function for the integrated model can then be obtained by summing the log-likelihood components for the three data sources. A method for incorporating a seasonal growth pattern into the analysis is presented. The integrated model, with and without a seasonal component, is applied to SBT data using two different growth curves, and the results are presented and discussed.

Methods

We adopted a maximum likelihood approach to jointly analysing the three sources of growth information. For each data source, we developed a statistical model and a log-likelihood function for fitting the model. The log-likelihood components were then added together to obtain a final objective function that could be optimized to estimate the model parameters. The addition of log-likelihood components is an appropriate procedure provided that the data from the different sources are independent, which is a reasonable assumption in this situation.

An important feature of any growth model is the functional form for the relationship between fish length (l) and age (a). In the derivation of the integrated model, we will leave the model very general by assuming a generic growth curve of the form

$$(1) \qquad l(a) = L_\infty f(a - a_0; \theta)$$

where L_∞ is asymptotic length and f is a monotone increasing function with parameter set $\{a_0, \theta\}$ that approaches 1 as $a \to \infty$ and equals 0 when $a = a_0$. We can think of a_0 as the theoretical age at which a fish would have had length 0 if we were to project its growth curve backwards. For the familiar von Bertalanffy (VB) curve, $\theta = \{k\}$ and $f(a - a_0; k) = 1 - \exp(-k(a - a_0))$. As would be expected in an integrated growth model, we assumed a common growth function f

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throughout the model components for the different data sources.

Incorporating seasonality

Many species, including SBT, exhibit a seasonal growth pattern, with the growth rate being faster during certain periods of the year. A seasonal component can be incorporated into any growth function by adding an annually periodic function, $S(\cdot)$, to the independent age variable. Explicitly, in the general growth equation given in eq. 1, $a - a_0$ can be replaced with $a - a_0 + S(t)$, where t is the fractional time of year since 1 January. In the tag–recapture data, we know the date of release and recapture so we can calculate t for both events. Similarly, we know the date of catch for the direct aging data. For each mode in the length–frequency data, we use the midpoint of the sample period as the catch date.

We considered a sinusoidal function for the seasonal effect, parameterized as

$$(2) \qquad S(t) = \frac{u}{2\pi}\sin(2\pi(t - w))$$

where u is the amplitude and w is the phase. The amplitude is constrained to be between 0 and 1 to prevent negative growth, whereas we constrained the phase to be between –0.5 and 0.5. Any bounds with a span of 1 could have been chosen due to the periodicity of the function. The rate of growth is maximal at $t = w$ and diminishes symmetrically about w to a minimum at $t = w - 0.5$ and $t = w + 0.5$.

Tag–recapture component

We used the maximum likelihood method of Laslett et al. (2002) to analyse the tag–recapture data. This method is based on estimating the joint density of the lengths at release and the lengths at recapture rather than modelling the length increments. In brief, a fish is tagged at time t_1 with release length l_1 and recaptured at time t_2 with length l_2, all of which are known. Define $A = t_1 - t_0$, where t_0 is the theoretical time at which a fish has length zero (analogous to the parameter a_0 on the age scale). Then A is a random variable, which is assumed to have density $p(\cdot)$ and whose parameters will be estimated in the model. In our application to SBT, we assume that A has a lognormal distribution with mean and standard deviation on the log scale of $\mu_{\log A}$ and $\sigma_{\log A}$, respectively; however, a more complex distribution such as a mixture model could be chosen (Laslett et al. 2002).

Although the age at release is unknown, if we denote it by a_1, then A is equivalent to $a_1 - a_0$. Similarly, $A + t_2 - t_1$ is equivalent to $a_2 - a_0$, where a_2 denotes the age at recapture. We introduce this notation to be consistent with the formulation of the growth function presented in eq. 1. Thus, the models for the release and recapture lengths can be expressed respectively as

$$l_{1i} = L_{\infty,i}\, f(A_i;\theta) + \varepsilon_{1i}$$

$$l_{2i} = L_{\infty,i}\, f(A_i + t_{2i} - t_{1i};\theta) + \varepsilon_{2i}$$

where i indexes fish. The asymptotic length is allowed to vary from fish to fish by modelling L_∞ as a random normal effect with mean μ_∞ and standard deviation σ_∞. The terms ε_1 and ε_2 represent measurement error. Note that the expression "measurement error" as used throughout this paper actually encompasses several sources of variation. Although measurement error is one principal source of variation in length, there may also be random variations due to environmental factors and genetic factors not captured by the random L_∞ parameter. Without further knowledge, we cannot separate this pooled source of error into its various components. We assume that ε_1 and ε_2 are independent of L_∞ and A as well as independent within and between fish (i.e., $\mathrm{cov}(\varepsilon_{1i}, \varepsilon_{2i}) = 0$ for all i, and $\mathrm{cov}(\varepsilon_{ki}, \varepsilon_{kj}) = 0$ for all $i \neq j$, $k = 1, 2$). Furthermore, we assume that they are both normally distributed with mean 0 and variance appropriate for the situation. For SBT, we assume that the variance of the measurement error depends on the length measurer. In particular, we assume that the variance is σ_s^2 if a trained scientist or researcher measured the length, and we allow for an additional component, σ_f^2, if an untrained fisher or factory staff measured the length because we expect measurements made by trained scientists to be more accurate. Note that scientists measured all release lengths. Thus, we can specify the variances of ε_1 and ε_2 by

$$V(\varepsilon_1) = \sigma_s^2$$

$$V(\varepsilon_2) = \begin{cases} \sigma_s^2 & \text{if measured by a scientist} \\ \sigma_s^2 + \sigma_f^2 & \text{if measured by a fisher} \end{cases}$$

Although these error variances are specific to SBT data, the method is very flexible with regard to the choice of variance functions.

If we condition on A, then l_{1i} and l_{2i} are both the sum of random normal variables and their joint distribution, $h(l_{1i}, l_{2i} \mid a)$, is bivariate normal (see Laslett et al. (2002) for the explicit formula). Their unconditional joint density can then by obtained by integrating over A:

$$h(l_{1i}, l_{2i}) = \int h(l_{1i}, l_{2i} \mid a)\, p(a)\, \mathrm{d}a$$

The product of the joint densities over all fish gives the likelihood function for the tag–recapture data. Thus, the negative log-likelihood function can be expressed as

$$(3) \qquad -\ln(\lambda_1) = -\sum_i \ln h(l_{1i}, l_{2i})$$

Length–frequency component

The method used to analyse the length–frequency data is described in detail in Laslett et al. (2004*a*). This method entails a two-step procedure. First, a Gaussian mixture model is used to decompose each length–frequency sample into age classes. In particular, an estimate of the mode and an accompanying standard error are generated for each age class assumed to be present in the sample. For SBT, the length data have been aggregated half-monthly so a sample corresponds to a half-month. Second, the summary statistics from the first step are inputted into the likelihood component for the length–frequency growth model.

In the first step, the length–frequency data from each sample is assumed to be a mixture of Gaussian components. The choice of a Gaussian distribution is supported in the case of SBT by visual inspection of the data. It is likely to be reasonable for many species; however, a different distribution can be used if it appears to be more appropriate. The Gaussian mixture model is fitted using maximum likelihood. The number of components to be fitted and the age classes to which they

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correspond need to be specified. As age increases, the components will tend to become indistinguishable. For SBT, they are generally quite distinct up to age 5, and the age classes to which they correspond are usually clear based on our knowledge of plausible lengths at age (e.g., from otolith data).

For each length–frequency sample, the parameters estimated are the mean (i.e., mode) and standard deviation of each Gaussian component and the proportion of lengths belonging to each component (with the constraint that they sum to 1). We assume that the standard deviations of the components are the same value for all components within a sample, but this value is allowed to differ between samples. This assumption can be relaxed; however, it will increase the number of parameters to be estimated and may not be practical. The estimation of the modes is unconstrained except for simple bound constraints. This differs from Leigh and Hearn (2000), who constrained mean growth over a season to be linear, and from Schnute and Fournier (1980), who constrained the means to follow a VB growth curve. A standard error associated with each mode is calculated by inverting the observed information matrix.

In the second step, we model mean fish length using the estimated modes and standard errors from the first step. Let i index the year, j the sample, and k the age class of the mode. The estimated mean length for a mode and its associated standard error are denoted by $\hat{\mu}_{ijk}$ and s_{ijk}, respectively. We estimate a decimal age, a_{ijk}, for each mode based on the age class of the mode and the fractional time of year between the midpoint of the sample period and the average day of birth for the species. If a species has a restricted and symmetric spawning period, then the midpoint of the spawning period should be a reasonable average birthday to use. An explicit example of assigning ages to the modes is given later when we apply the model to SBT. In the growth model, we make the simplifying assumption that the a_{ijk}s have no error. The degree to which this assumption is violated for a given a_{ijk} will depend on how much the average birthday of fish in component i, j, k differs from the average birthday assumed and, to a lesser extent, on how much the average catch date of fish in the component differs from the midpoint of the sample period.

The growth model can be expressed as

$$\hat{\mu}_{ijk} = \mu_\infty f(a_{ijk} - a_0;\theta) + e_{ijk} + \varepsilon_{ijk} \quad (4)$$

where e and ε are independent random effects representing sampling error and residual model error, respectively. We assume that $e_{ijk} \sim N(0, s_{ijk}^2)$, where s_{ijk} is the known standard error estimate from the first step, and $\varepsilon_{ijk} \sim N(0, \sigma_\varepsilon^2)$. The parameter μ_∞ represents the average asymptotic length of a group of fish. There is almost no information from the length–frequency data on the mean asymptotic length of fish, let alone the variance, so we model μ_∞ as a fixed effect. Note the contrast with the tag–recapture model where L_∞ represents the asymptotic length of an individual fish and is modelled as a random effect. This issue is discussed further in the Integrated model section below.

The negative log-likelihood corresponding to model 4 is given by

$$-\ln(\lambda_2) = \frac{1}{2}\sum_i\sum_j\sum_k\left[\ln(2\pi V(\hat{\mu}_{ijk})) + \frac{(\hat{\mu}_{ijk} - E(\hat{\mu}_{ijk}))^2}{V(\hat{\mu}_{ijk})}\right] \quad (5)$$

where

$$E(\hat{\mu}_{ijk}) = \mu_\infty f(a_{ijk} - a_0;\theta)$$

and

$$V(\hat{\mu}_{ijk}) = s_{ijk}^2 + \sigma_\varepsilon^2$$

Direct age–length component

In modelling the direct aging data, we assign an age to each fish based on the number of annual growth bands counted in its hard part (e.g., its otolith for SBT). We assume that all fish are born on the same day of the year, say b (regardless of the year). Let n be the band count, r the day of capture, and d the day of band formation, where both r and d are expressed as number of days since b. Then, a decimal age, a, can be assigned to each fish as follows:

$$a = \begin{cases} n + r/365 & \text{if } r < d \\ n - 1 + r/365 & \text{if } r \geq d \end{cases} \quad (6)$$

If a fish has already formed a new growth band in the time between its last birthday and its day of capture, then its integer age is $n - 1$; otherwise, its integer age is n (assuming that the band count is correct). Thus, the age calculated in eq. 6 is simply the fish's integer age plus the fraction of the year between its birthday and its day of capture.

The capture day is generally known precisely, and although the band counts are subject to errors, we assume they are not biased and that the aging methodology has been designed to minimize uncertainty. For example, with SBT, multiple band counts are made before assigning a final value (Gunn et al. 1996). The day of band formation and the day of birth will not be known exactly, and they will almost certainly vary between fish and years. Appropriate average values need to be determined for the species being studied. As stated for the length–frequency data, the estimated midpoint of the spawning season will often be a reasonable value to use as an average birthday. The ability to estimate a reasonable average day of band formation will depend on how variable the time of band formation is for the species in question and the amount of information known regarding band formation. These issues are discussed in the case of SBT when we later apply the model to SBT data.

Despite the uncertainties, the decimal ages calculated using eq. 6 are treated as exact in the model. If the error distribution for the band counts is symmetric and the values chosen for the average birthday and the average day of band formation are close to the true averages, then the age estimates and, consequently, the growth parameter estimates should not be biased. However, the precision of the parameter estimates will be unrealistically high. Some preliminary approaches for modelling the errors in age were explored in appendix 12 of Polacheck et al. (2003), but these approaches are still in the developmental stage and require further work before being incorporated into the integrated model.

Let l and a denote the length and age of a fish, respectively; then, the model can be expressed as

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Table 1. Summary of the parameters estimated in the various model components (as indicated by ×).

	Parameter											
Model component	μ_∞	σ_∞	θ	u	w	$\mu_{\log A}$	$\sigma_{\log A}$	a_0	σ_s	σ_f	σ_ε	σ_γ
Tag–recapture	×	×	×	×	×	×	×		×	×		
Length–frequency	×		×	×	×			×			×	
Direct age–length	×	×	×	×	×			×				×

$$l_i = l_{\infty,i}\, f(a_i - a_0;\theta) + \gamma_i$$

where i indexes fish; γ represents measurement error (and other unknown model error) and is assumed to be normally distributed with mean 0 and standard deviation σ_γ. As with the tag–recapture data, the asymptotic length is allowed to vary between fish by modelling L_∞ as a random normal effect with mean μ_∞ and standard deviation σ_∞. We assume that L_∞ and γ are independent. The negative log-likelihood is given by

$$(7) \qquad -\ln(\lambda_3) = \frac{1}{2}\sum_i \left[\ln(2\pi V(l_i)) + \frac{(l_i - E(l_i))^2}{V(l_i)}\right]$$

where

$$E(l_i) = \mu_\infty\, f(a_i - a_0;\theta)$$

and

$$V(l_i) = \sigma_\infty^2\, f(a_i - a_0;\theta)^2 + \sigma_\gamma^2$$

Integrated model

The overall objective function to be optimized, which we will denote by Λ, is simply the sum of the three negative log-likelihood functions given in eqs. 3, 5, and 7:

$$(8) \qquad \Lambda = -(\ln(\lambda_1) + \ln(\lambda_2) + \ln(\lambda_3))$$

The parameters that are common between model components and those that are unique to individual components are summarized in Table 1. The asymptotic variance parameter σ_∞ is common to just the tag–recapture and direct aging components. For the length–frequency component, we are not modelling lengths of individual fish, but rather, we are modelling mean lengths (see eq. 4). As such, we expect the asymptotic length parameter to have the same mean but not the same variance as the asymptotic length parameter in the tag–recapture and direct aging models. There is no information in the length–frequency data on fish approaching their asymptotic length with which to estimate the relevant asymptotic variance parameter, so we modelled the asymptotic length as a fixed effect for this component. Whether the asymptotic length is assumed to be random or fixed will have virtually no effect when modelling the young ages available from length–frequency data. The parameter a_0 is not estimated in the tag–recapture component because it is already encompassed in the random variable A (recall that $A = a_1 - a_0$).

Approximate standard errors for the parameter estimates can be computed by evaluating the inverted observed information matrix $\{\partial^2\Lambda/\partial\theta_i\partial\theta_j\}^{-1}$, where θ is the vector of parameters, at the minimum of the negative log-likelihood function, Λ.

Results

In this section, we apply the integrated growth model to SBT data. We first describe the data sets, then discuss the choice of growth function, and finally present the results.

SBT data

Although information on the growth of SBT exists from the 1950s until the present, only data for fish that experienced early years of growth in the 1980s are included in this paper. Previous studies using incremental length data from tag–recapture studies (Hearn and Polacheck 2003) and modal analysis of length–frequency data (Leigh and Hearn 2000) have found that the average growth rate of SBT increased between the 1960s and the 1980s. An analysis of growth using all of the data combined would give an estimate of average growth over the entire time period, which is not very informative given the temporal changes. A meaningful analysis of all years' data would require a model that allows for changes in growth over time; the development of such a model is the topic of a future paper. We chose to analyse the 1980s data for several reasons: extensive data sets exist in this decade for each of the data sources: there is a large degree of overlap among the data sets with respect to ages and lengths of SBT; and growth appears to have been relatively stable over this time period. Thus, the 1980s provided the best data for testing the integrated methods.

Tag–recapture data

Extensive SBT tag–recapture experiments were conducted by CSIRO Marine Research from the 1960s through the 1990s. During the 1980s (in the years 1980, 1983, and 1984), 10 741 juvenile SBT between the ages of 0 and 4 were caught and tagged with conventional spaghetti tags. The fish were measured for length and then released back into the wild. A complete description of the tagging operations is given in Majkowski (1982).

By January 2002, there were 2181 recaptures from fish tagged in the 1980s with reliable release and recapture information for studying growth (see appendix 3 of Polacheck et al. (2003) for details of the screening process). Of these fish, the release lengths ranged from 40 to 115 cm and the recapture lengths from 47 to 173 cm. The distribution of the times at liberty was highly skewed towards shorter times at liberty and ranged from 30 days to 4356 days (~12 years) with a median value of 340 days. Note that the minimum of 30 days at liberty was imposed by the screening process to allow for an initial effect of tagging on fish growth. We assume that, in terms of length, this initial effect will be negligible after 30 days (William S. Hearn, CSIRO Marine Research, P.O. Box 20, North Beach 6020, Western Australia, personal communication). A plot of the change in length versus time at liberty is shown in Fig. 1. Growth information on older

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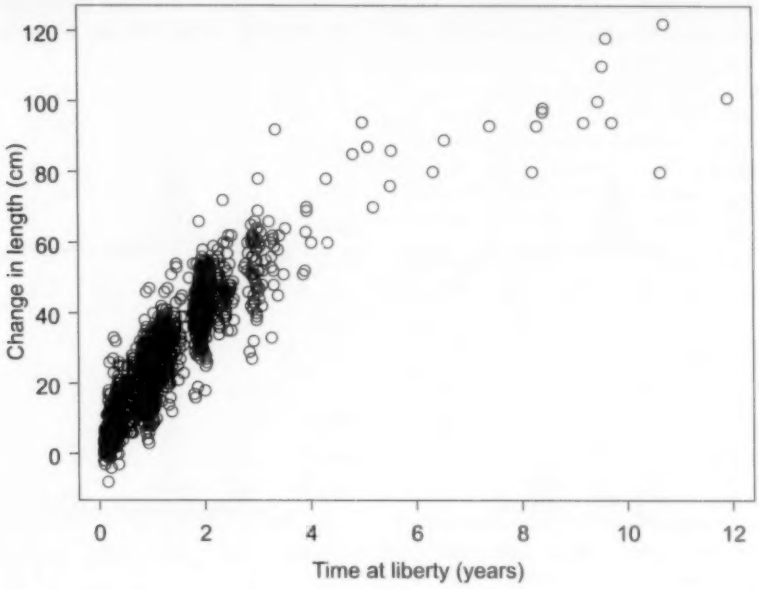
Fig. 1. Southern bluefin tuna (*Thunnus maccoyii*) tag–recapture data for fish released in the 1980s (only data remaining for analysis after screening are shown).



fish tends to be lacking because only juvenile fish were tagged and most of them had relatively short times at liberty.

Length–frequency data

Length–frequency data from fish caught during the 1980s in the South Australian surface fishery were included in our investigation. Although length data exist for the Western Australian and New South Wales fisheries, as well as the Japanese longline fishery, there are problems unique to each of these data sets with regard to studying growth (see Polacheck et al. 2003). The South Australian data are most abundant and most consistent for modal analysis. Length samples were taken from individual landings at either the place of landing or the place of processing. Sampling protocols were designed to avoid introducing biases into the selection of fish to be measured. The length–frequency sample data were aggregated by half-months and scaled up to represent the total catch in a half-month rather than just the sampled catch. For details of the sampling procedure and the scaling up of the sample length–frequencies, refer to Majkowski (1982), Majkowski and Morris (1986), and Deriso and Bayliff (1991). The half-monthly length–frequency distributions exhibit distinct modes that presumably correspond to age classes (Fig. 2), and the progression of these modes over the year provides information on growth.

The fishery in South Australia generally operates within the period November–July, so it is more practical to track the progression of modes over a fishing season than over a calendar year. As such, the 24 half-months in a year are indexed by −4, −3,..., 19 starting in the first half of November and ending in the last half of October. Because the length–frequency data have been scaled up to represent the total catch in a half-month, using these data as the raw data in our analysis would not be correct from a statistical viewpoint, since the actual sample sizes are much smaller than the catch sizes and varied among years. Obtaining the raw sampling data proved problematic. Thus, to correct for the scaling up, we adopted the scale factors proposed by Leigh and Hearn (2000). The recorded frequencies in each half-month were divided by the scale factor for that half-month to give the "effective" sample frequencies (i.e., estimates of the numbers of independent length measurements in each length class). The total "effective" sample size in a half-month ranged from a few fish to several thousand. The lengths of fish ranged from 38 to 200 cm, but 99% of the lengths were less than 125 cm. We only included fish of length 130 cm or less in our analysis because modes cannot be confidently distinguished beyond this length.

Direct age–length data

Methods for directly aging SBT from their otoliths were developed and verified in the 1990s (Gunn et al. 1996; Clear et al. 2000). Since the late 1980s, extensive collection of otoliths from SBT has been undertaken. Otoliths have been collected from juvenile fish landed in the Australian surface fishery and caught during tagging expeditions and from older fish caught by Japanese longline vessels operating in the Australian Exclusive Economic Zone and on the high seas. Additionally, a large number of otoliths have been collected in recent years from fish landed in Indonesia from longline vessels operating on the spawning grounds. Approximately 4500 of the collected otoliths have been aged by trained and experienced staff. More details of the direct aging data can be found in appendix 3 of Polacheck et al. (2003).

Not all of the data were considered suitable for inclusion in our analysis. Data from the spawning grounds for fish younger than 15 years were excluded because there is strong evidence of size selectivity in spawning within an age class for ages 14 years and below (Farley et al. 2001). In addition, the period when bands can form in the otoliths of SBT

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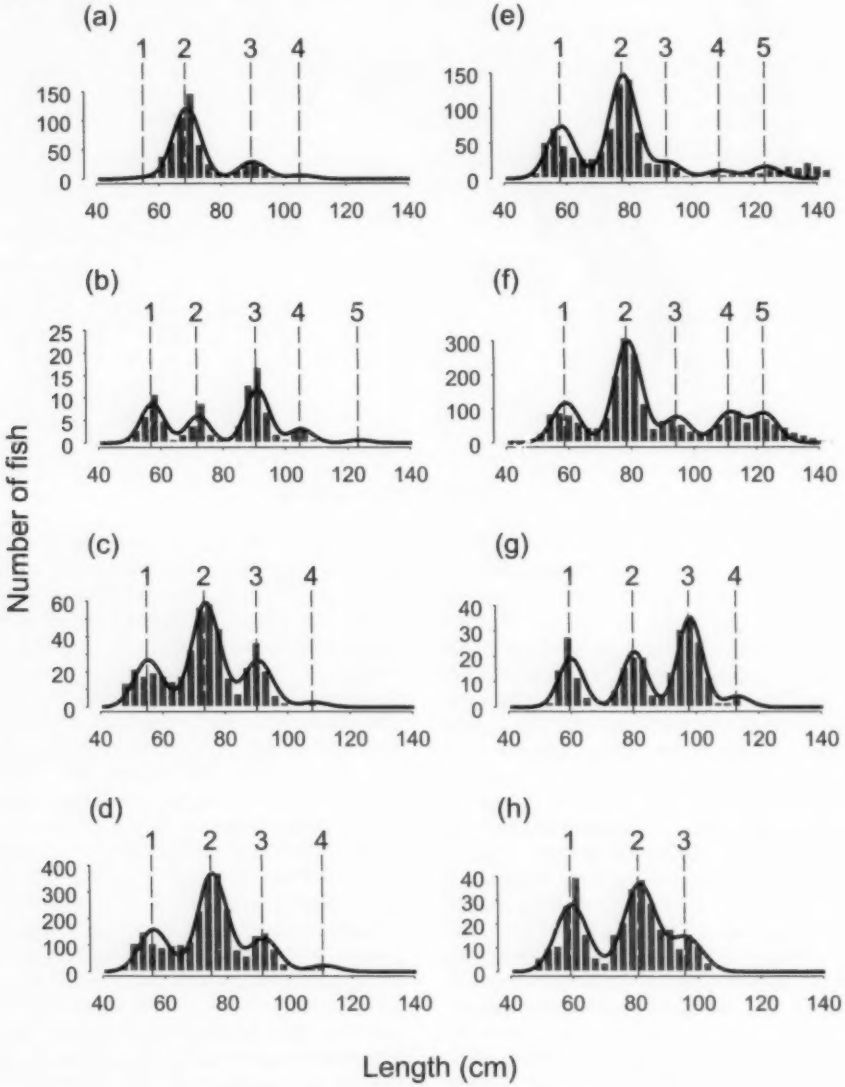
Fig. 2. Length–frequency data collected from commercial catches in the South Australia surface fishery in the 1983 season (grouped in 3-cm length bins): *a*–*h* correspond to half-months –1 to 6 (i.e., first half of December 1982 to last half of March 1983). The solid lines show the fitted Gaussian mixture models, the broken vertical lines mark the fitted modes, and the integers above the broken lines give the age class of fish in that component. Average growth of fish in an age class can be estimated by tracking the change in the modal length of that age class over time.



extends from May through September (appendix 11 of Polacheck et al. 2003), and we cannot be sure whether a fish caught during this period has yet deposited a band. As such, SBT caught during the winter months of May–September were omitted because there is an uncertainty of plus or minus 1 year in their age estimates. This omission should not induce biases into the growth parameter estimates; however, it will result in them having higher variance. This issue is discussed later in the Results section.

The number of direct age–length observations for fish born in the 1980s that were available for analysis was 688. The year of birth was estimated from the catch year and the number of annual bands in the otolith. The band counts ranged from 1 to 21 and the lengths of fish ranged from 45 to 200 cm. SBT from all geographical areas where fishing occurs were represented; however, the majority of data were from older fish caught on the Indonesian spawning grounds (Table 2).

Choice of growth function

To apply the integrated growth model to the SBT data, a growth function must be selected. Initially, we used the growth function corresponding to the traditional VB curve:

$$(9) \qquad f(a - a_0; k) = 1 - e^{-k(a-a_0)}$$

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Table 2. Numbers of otoliths from southern bluefin tuna (*Thunnus maccoyii*) born in the 1980s that were used in our analyses, broken down by age (i.e., otolith band count) and area of capture.

	Age estimate (otolith band count)																					
Area	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Total
South Australia	4	52	34	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	94
Indonesia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	89	61	76	67	51	33	1	378
New Zealand	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2
Southeast Indian Ocean	0	0	0	8	9	12	6	7	3	5	1	3	3	0	0	0	0	0	0	0	0	57
South Africa	0	0	0	10	13	3	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	31
Tasmania	0	1	16	8	10	7	7	2	5	5	4	0	4	0	0	1	0	0	0	0	0	70
Western Australia	19	11	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	36
Total	23	64	55	31	32	22	15	10	9	12	6	3	7	0	89	62	76	67	51	33	1	668

The VB curve is the most commonly used growth function in fisheries literature. However, previous analyses suggest that SBT growth is better described by a function that allows for a transition in the growth pattern during the juvenile life stage (Laslett et al. 2002; Hearn and Polacheck 2003). Studies of Pacific northern bluefin tuna (*Thunnus thynnus*) suggest that this species also exhibits a transition in growth during its life cycle (Bayliff et al. 1991). Hearn and Polacheck (2003) discussed possible reasons for this phenomenon; they hypothesized that it may be due to the dual nature of the life history for most tuna species. In the case of SBT, juveniles are found in dense schools in surface waters close to shore, whereas older fish are generally found in offshore waters at greater depths.

Hearn and Polacheck (2003) modelled SBT growth as a two-stage process in which the growth in each stage follows a different VB curve, such that there is a discontinuity in the growth rate at the transition between the two stages. Laslett et al. (2002) developed an alternative growth curve that allows for a smooth transition between two VB curves with different growth rate parameters. The curve is called the VB growth curve with a logistic growth rate (abbreviated VB log k) to reflect the fact that the change in growth rate is modelled using a logistic function. The growth function for the VB log k model is given by

$$(10)\quad f(a-a_0;\{k_1,k_2,\alpha,\beta\}) = 1-e^{-k_2(a-a_0)}\left\{\frac{1+e^{-\beta(a-a_0-\alpha)}}{1-e^{\alpha\beta}}\right\}^{-(k_2-k_1)/\beta}$$

As a increases, the function makes a smooth transition from a VB curve with growth rate parameter k_1 to a VB curve with growth rate parameter k_2. The parameter α governs the age at which the midpoint of the transition occurs, and β governs the rate of the transition (being sharper for larger values).

Parameter estimates

Before fitting the integrated model, we needed to fit Gaussian mixture models to the half-monthly length–frequency distributions to obtain the estimated modes and standard errors. We fit a maximum of five components per half-month. In most half-months, the allocation of components to age classes was unequivocal based on our knowledge of plausible lengths at age for such young SBT. The fits were most often very good (see Fig. 2), but they could be poor in some cases. In particular, when the sample sizes were small, the fits appeared to be little more than mathematical artefacts. Thus, we only carried forward the summary data for a component into the growth model if the estimated number of fish in the component was greater than 50 (50 was chosen somewhat arbitrarily after looking at the distribution of sample sizes). The estimated number of fish in a component was obtained by multiplying the effective sample size for the period by the estimated proportion of fish in the component (which was obtained in the first step). Furthermore, we only included data for age classes 1–4 in the growth model even though a fifth mode was sometimes fitted. When a fifth mode was fitted, it acted as a catchall for any data beyond age 4 and likely encompassed data from several age classes. A plot of the summary

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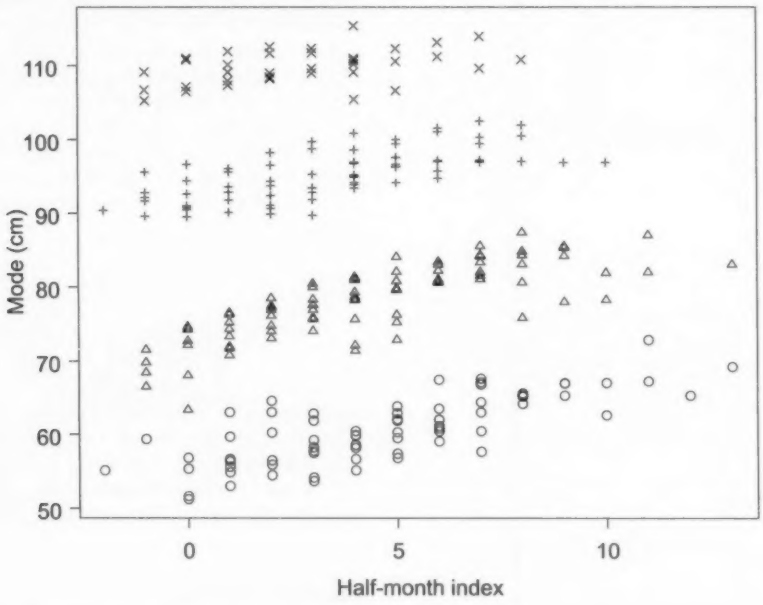
Table 3. Parameter estimates from applying the integrated growth model to 1980s southern bluefin tuna data.

		Parameter estimate					
Growth curve	Omit age 1?	μ_∞	σ_∞	k_1	k_2	α	β^a
VB	No	179.7 (0.43)	6.1 (0.22)	0.21 (0.002)			
VB log k	No	184.9 (0.81)	7.8 (0.26)	0.22 (0.003)	0.17 (0.004)	2.9 (0.09)	30.0 (na)
VB log k	Yes	183.9 (0.75)	8.4 (0.27)	0.24 (0.005)	0.18 (0.004)	2.5 (0.11)	30.0 (na)
Seasonal VB log k	No	184.7 (0.80)	8.1 (0.26)	0.22 (0.004)	0.17 (0.004)	2.8 (0.12)	18.3 (na)
Seasonal VB log k	Yes	183.8 (0.73)	8.7 (0.27)	0.24 (0.004)	0.18 (0.003)	2.5 (0.08)	30.0 (na)

Note: Results are for various growth curves and data subsets, as specified. Standard error estimates for the parameter estimates are given in parentheses; [a]β constrained to be ≤ 30.

Fig. 3. Fitted modes for age classes 1–4 in the 1980s plotted against half-month. Age classes 1, 2, 3, and 4 are plotted as ○, △, +, and ×, respectively. Growth within an age class appears to be fastest prior to half-month 5, after which it slows, suggesting a seasonal pattern to growth. This pattern is most evident for age classes 1 and 2.



modes used in the growth model versus the half-month index is shown in Fig. 3. The separation of modes into age classes is evident in this figure, and the seasonal pattern of growth can be seen by the more rapid increase in length over the austral summer (half-months 0–5) before slowing down around mid-March (half-month 6). This pattern is most apparent for age groups 1 and 2.

To assign decimal ages to the modes, we assumed that SBT have a birthday of 1 January. This value is a reasonable midpoint of the spawning season based on catch data from the spawning grounds (Davis and Nurhakim 2001), and it has been advocated in other studies (Leigh and Hearn 2000). Thus, fish belonging to age class k and half-month j were allocated a final mean age of $k + (j - 0.5)/24$, $j = -4, -3, ..., 19$ (recall that a fishing season starts in November, indexed by half-month −4).

We assigned decimal ages to individuals in the direct aging data using eq. 6. Again, we assumed an average birthday of 1 January. To estimate an average day of band formation was more difficult because the time of band formation is so variable for SBT. Recall that we omitted fish from the feasible period of band formation (May–September). By doing so, we could be quite confident whether or not a fish had formed a band between 1 January and its day of capture. This omission should not induce biases into the growth parameter estimates; it will, however, increase the variance of the parameter estimates. We could have used 1 July as an approximate midpoint of the period of band formation (appendix 11 of Polacheck et al. 2003), but this date is a very rough estimate based on limited data. If the distribution of the days of band formation is not symmetric about this day, then the age errors would be biased. Thus, we opted to take the more conservative approach of omitting uncertain data.

The integrated model was fitted to the SBT data using both the VB and VB log k growth functions specified in eqs. 9 and 10, respectively. Parameter estimates were obtained by minimizing the objective function in eq. 8. The optimization was unconstrained except for generous upper and lower bounds on all parameters. The estimate of the mean asymptotic length is somewhat higher in the VB log k model than in the VB model (Table 3). The initial rate of growth in the VB log k model is very similar to the growth rate in the VB model;

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u	w	$\mu_{\log A}$	$\sigma_{\log A}$	a_0	σ_s	σ_f	σ_ε	σ_γ
		0.66 (0.008)	0.17 (0.003)	–0.57 (0.019)	2.7 (0.12)	4.5 (0.26)	4.2 (0.20)	5.5 (8.77)
		0.58 (0.012)	0.17 (0.003)	–0.44 (0.025)	2.3 (0.12)	4.3 (0.23)	4.4 (0.21)	4.5 (7.18)
		0.52 (0.018)	0.17 (0.003)	–0.18 (0.039)	2.3 (0.13)	4.1 (0.23)	2.6 (0.14)	4.1 (na)
0.34 (0.042)	0.13 (0.016)	0.58 (0.015)	0.17 (0.003)	–0.43 (0.028)	2.1 (0.12)	4.2 (0.22)	4.3 (0.20)	4.6 (7.27)
0.35 (0.040)	0.12 (0.014)	0.52 (0.015)	0.17 (0.003)	–0.18 (0.033)	2.0 (0.12)	4.0 (0.21)	2.5 (0.14)	4.1 (na)

na indicates that the parameter was regarded as known. VB, von Bertalanffy; VB log k, von Bertalanffy with a logistic growth rate.

Table 4. Negative log-likelihood and Akaike information criterion (AIC) values for the various model fits.

Growth curve	Omit age 1?	Number of parameters	–log likelihood	AIC
VB	No	10	17 752.1	35 524.1
VB log k	No	13	17 649.5	35 325.1
VB log k	Yes	13	17 259.1	34 544.2
Seasonal VB log k	No	15	17 607.1	35 244.3
Seasonal VB log k	Yes	15	17 209.1	34 448.2

Note: VB, von Bertalanffy; VB log k, von Bertalanffy with a logistic growth rate.

however, the VB log k model suggests that the growth rate slows considerably between ages 2 and 3. This age of transition is consistent with the average age when juveniles start to migrate offshore. Recall that α is the age of transition relative to a_0, so we estimate the midpoint of the transition to be at age $\alpha + a_0$. Any value of β over 10 implies an almost instantaneous transition between the two growth phases, so the fact that β converged to the preset upper bound of 30 suggests that the rate of transition is very fast.

According to the Akaike information criterion (Akaike 1974), the VB log k fit is significantly better than the VB fit (Table 4). To further evaluate how well the two models fit the data, we calculated residuals (fitted minus observed length) for each of the data sets. When the model involved a random L_∞, we calculated the fitted values according to the estimated mean growth curve (i.e., using $\hat{\mu}_\infty$). To calculate the fitted release and recapture lengths in the tag–recapture data, we required a realised value of A for each fish. A natural approach is to use the mean of the posterior distribution for A conditioned on the fish's release and recapture lengths. However, this approach yields biased estimates of A (appendix 5 in Polacheck et al. 2003), so we used the approximately conditionally unbiased estimator $\tilde{A}_f$ described in Laslett et al. (2004*b*) instead.

The improvement in the fit of the VB log k model over the VB model is evident in an examination of the residuals (Figs. 4 and 5). For the direct aging component, the VB model overestimates the length of middle-aged fish (around ages 5–12); this is corrected by using the VB log k model. A local linear smooth of the recapture length residuals for the VB model shows a pattern in which the length of younger fish is underestimated and the length of older fish is overestimated; the transition occurs between recapture "ages" 3 and 5 (recall that this is age relative to a_0). This pattern lends support to a two-stage growth function, such as the VB log k curve. The recapture residuals for the VB log k model show no such pattern. The release residuals are also improved slightly in the VB log k model. The length–frequency residuals are more complicated. In both models, the predominant feature of the residuals is the underestimation of age class 1 and the overestimation of age classes 2–4. However, overlooking this general lack of fit, which we discuss below, the fit to the 4-year-olds is better in the VB log k model.

SBT are spawned in the northeast Indian Ocean between Indonesia and the northwest coast of Australia, generally between the months of September and April. Catches indicate that there tends to be two peak spawning times, one around September–October and one around January–February, although there is a high degree of variability between years (Davis and Nurhakim 2001). Juveniles migrate southward along the west coast of Australia, and then a large percentage of them travel eastward along the south coast of Australia to the Great Australian Bight. If SBT are spawned at two peak times, then we might expect to find the larger earlier-spawned fish off South Australia at the same time that we find the smaller later-spawned fish off Western Australia. Our method of assigning ages assumes that all fish are spawned on the same day, so this age difference cannot be captured. Because all of the length–frequency data are from South Australia, the length data for 1-year-olds will be biased towards bigger fish. This is evident in the model fits.

We assigned ages to both the length–frequency data and the direct aging data assuming a birthday of 1 January. This introduces an uncertainty of several months into the age depending on the true time of spawning. This is primarily a problem for very young fish whose growth is rapid enough that an age difference of a few months translates into a significant difference in length. The model for the tag–recapture data incorporates the estimation of the age at release and hence has the ability to deal with variable spawning times by assigning suitable ages based on size (i.e., small fish will be considered younger than bigger fish caught at the same time). Ideally, we would like the model components for the length–frequency and direct aging data to incorporate this uncertainty

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Fig. 4. Residual length (observed minus fitted) for the integrated von Bertalanffy model for (*a*) direct aging, (*b*) length–frequency, (*c*) tagging release, and (*d*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns.

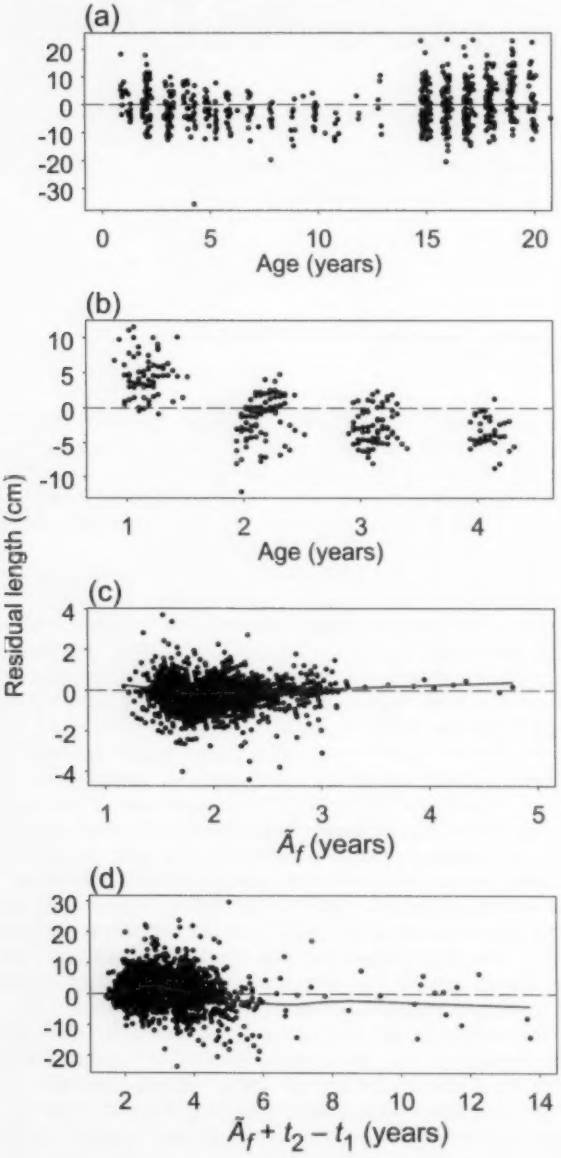
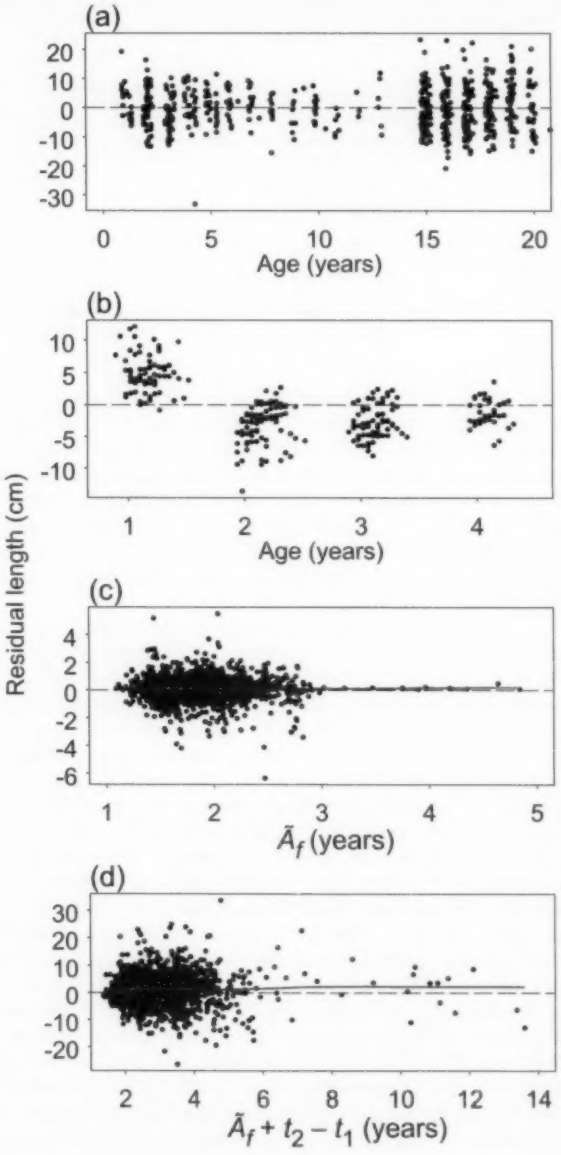


Fig. 5. Residual length (observed minus fitted) for the integrated von Bertalanffy log k model for (*a*) direct aging, (*b*) length–frequency, (*c*) tagging release, and (*d*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns.



as well. Some preliminary approaches for doing so have been explored in Polacheck et al. (2003), but they require further investigation.

As an immediate and unbiased approach to dealing with the problem, we refit the integrated VB log k model leaving out the length–frequency data for age class 1 and the direct aging data for fish with an estimated age of less than 1.5 years. Our justification for doing so is that the uncertainty in age has the most significant effect on the expected length of 1-year-old fish, with the effect diminishing exponentially with age. Moreover, the difference in length at age of fish caught off Western Australia and South Australia does not appear to persist past age 1. Perhaps the later-spawned fish catch up

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Fig. 6. Residual length (observed minus fitted) for the integrated von Bertalanffy log k model, excluding age-1 direct aging and length–frequency data for (*a*) direct aging, (*b*) length–frequency, (*c*) tagging release, and (*d*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns.

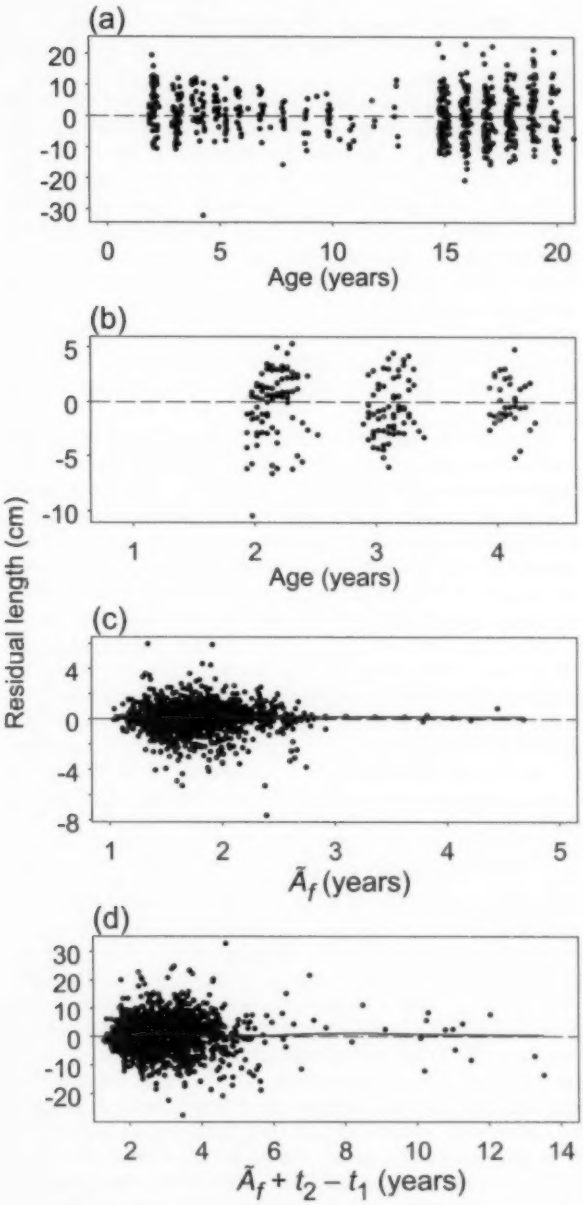
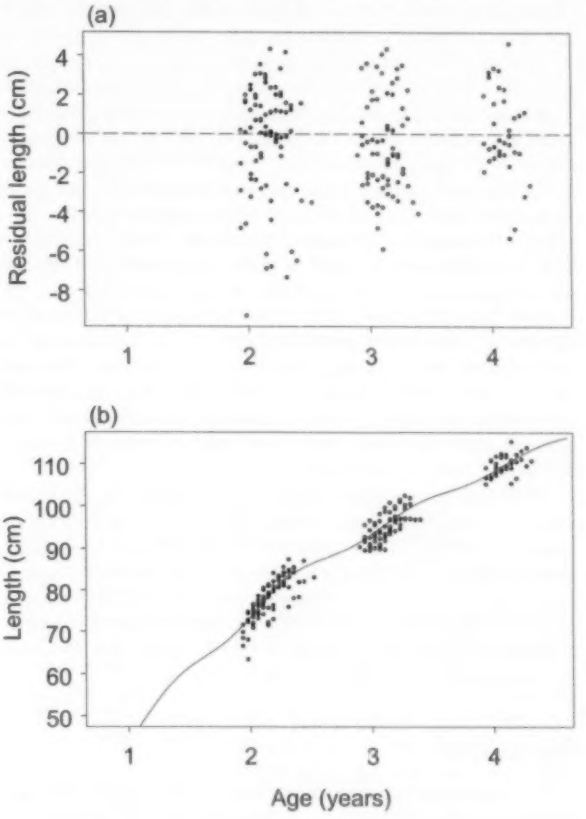


Fig. 7. Length–frequency diagnostic plots for the seasonal integrated von Bertalanffy log k model, excluding age-1 direct aging and length–frequency data. (*a*) Residual length (observed minus fitted); (*b*) fitted curve through the data to better display the seasonal pattern.



in size by age 2, or perhaps the fish from the two areas mix during their subsequent years of life so that the fish off Western Australia and South Australia no longer correspond to late- and early-spawned fish. Although the uncertainty in age is still present in fish older than age 1, we expect only an increase in the variance of their length at age (which will diminish rapidly with age) and not a bias. The largest impact on the estimated growth model of leaving out the 1-year-old length–frequency and direct aging data is that the initial stage of growth is steeper, as reflected by the increase in the parameters k_1 and a_0 (Table 3). The improvement in the fit to the length–frequency data is apparent in the residual plot for this data set; the fit to the other two data sets appears to be relatively unaffected (Fig. 6).

SBT experience a period of fast growth during the austral summer and slow growth during the austral winter (Hearn 1986). We see evidence of this in the length–frequency data, and it is the reason that SBT otoliths display annual growth bands (corresponding to slow winter growth). None of the models considered thus far capture this seasonality, and it is important to determine the effect of doing so on the parameter estimates and the model fit. Thus, we refit the VB log k model including the sinusoidal seasonal component given by eq. 2 to both the data including and excluding age-1 length–

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frequency and direct aging data. The estimates of the mean growth curves are almost identical to the mean curves estimated from fitting the nonseasonal VB log k model to the corresponding data (see the parameter estimates in Table 3). However, the estimates of the seasonality parameters, which are almost identical whether the age-1 data are included or not, suggest that there is an appreciable seasonal pattern to growth. The estimate of the phase, w, suggests that SBT experience their fastest growth in mid-February, which is consistent with our understanding that SBT growth is fastest during the austral summer. A comparison of the Akaike information criterion values between the seasonal and nonseasonal models fitted to the same data suggests that incorporating a seasonal component significantly improved the fits (Table 4). The improvement is visible in diagnostic plots for the length–frequency data (Fig. 7). This figure shows the results obtained without age-1 data, but the same observation applies for the model including age-1 data. Differences in the fit to the other two data sets cannot be seen visually (and thus, the diagnostic plots are not shown); however, the negative log-likelihood value for the tag–recapture component was reduced significantly for both the model with age-1 data and the model without age-1 data.

Approximate standard errors for the parameter estimates were obtained for each model fitted using the inverted observed information matrix (Table 3). When a parameter was estimated to be on the boundary of the parameter space, or the log-likelihood function was very flat with respect to a parameter, the parameter had to be regarded as known to obtain a positive definitive information matrix. This was the case for the parameter β and often for σ_γ.

Discussion

It is important to have a method for modelling growth that can incorporate all of the available data sources because any one data source does not usually contain complete information on growth over the entire life span of the species. Oftentimes, where one data set is deficient, another can provide valuable information. For example, in the case of SBT, the direct aging data contain information on older fish that is not available from the length–frequency or tag–recapture data, the length–frequency data have information on young fish and on seasonal growth, and the tag–recapture data are the only direct source of information on the growth of individuals, which is important for understanding variability in the growth process.

To better understand the contribution of each data set to the estimation of SBT growth, we refitted the seasonal VB log k model, first, leaving out the entire otolith data set and, second, leaving out the entire length–frequency data set. In both cases, all of the parameter estimates remained virtually unchanged (for the sake of brevity, we will only discuss the results in qualitative terms). This reflects the high degree of consistency among the three SBT data sets. It also suggests that the tag–recapture data set contains good information on seasonal growth, which is not obvious from just plotting the data (as it is for the length–frequency data). What does change by omitting data sets is our confidence in the parameter estimates. For example, when the otolith data set is omitted, the standard error estimates for μ_∞, k_1, and k_2 increase by an order of magnitude. When the length–frequency data set is omitted, the standard error estimates for k_1 and α increase, although only by very small amounts. For the SBT data sets used here, the amount of tag–recapture data on young fish is so great that the contribution of the length–frequency data to the overall likelihood function is small (the log-likelihood value for the length–frequency component is an order of magnitude smaller than that of the tag–recapture component). In situations where the tagging data are less abundant, we would expect the uncertainty in the parameter estimates of k_1, α, and especially the seasonal parameters u and w to increase significantly with the omission of the length–frequency data.

Data from all of the sources discussed will not always be available. An advantage of developing an integrated model of growth under a likelihood framework is the ease with which data sources can be excluded from, or included in, the model. If one of the data sources is not available for a species, then the likelihood component corresponding to the missing data set can be removed from the overall objective function. On the other hand, if a data set other than the three that we discussed exists, then it is possible to add on a likelihood component for this data set. Of course, the development of an appropriate model for these new data may not be trivial, and consideration must be given to independence among data sets.

To make the integrated model widely applicable, we formulated the model in terms of a generic growth function that approaches an asymptotic length (L_∞). We only allowed for individual variability in L_∞, but in theory, any or all of the growth parameters can be modelled as random effects. If the distribution for length (or the joint distribution for release and recapture lengths in the tagging component) is no longer apparent, the likelihood function for the component can be obtained by conditioning on the random parameter(s) and integrating. Note, however, that this may be too computer intensive to be feasible in practice. Alternatively, approximations may be used. For example, Sainsbury (1980) showed how to fit a VB model with a normally distributed L_∞ parameter and a gamma-distributed k parameter to age–length or length increment data using a normal approximation for the likelihood. In the case of SBT, visual inspection of the data as well as results from fitting standard VB curves with various error structures to tagging data (Hampton 1991; Polacheck et al. 2003) indicate that only including individual variability in L_∞ is sufficient. The results from applying the integrated model to SBT data strongly support the hypothesis that there is a significant seasonal component to SBT growth. We used a sinusoidal function to model the seasonal growth pattern. There is some suggestion in the length–frequency summary data that the growth of SBT is fastest over the summer season before levelling off sometime around May and remaining almost flat for the winter. Lack of data over the entire year makes the pattern difficult to confirm. If this were the case, an alternative seasonality function that is flatter over the winter could be more appropriate. Even so, the sinusoidal function appears to have performed adequately.

With regard to the direct aging data, research scientists and trained staff collect the otoliths and also measure the

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lengths of the fish. It would seem reasonable, therefore, to assume that the measurement error of lengths in the direct aging data should have the same variance as the measurement error for scientist-measured lengths in the tag–recapture data (i.e., $\sigma_\gamma = \sigma_s$). In our results, σ_γ is actually much greater than σ_s. The tag–recapture model estimates the age at release intrinsically, so the data points can be adjusted along the age axis to put them closer to the mean curve. For the direct aging data, we assign an age assuming a common birth date for all fish and take this age as precise. Therefore, it is not surprising that the residual variability in length at age (above and beyond the variation due to a random L_∞) is greater for the direct aging data than for the tag–recapture data.

The approximate standard errors calculated for the parameter estimates were generally very small. In part, this reflects the large amount of data contributing to the parameter estimates; however, there are several reasons why the standard errors may be underestimated. There is likely nonindependence in the data sets due to nonindependence among fish tagged in the same school in the tag–recapture data, overestimation of the effective sample size in the length–frequency data, possible reader biases in the otolith data, et cetera. Additionally, there may be lack of normality in the parameter estimates, and the choice of model error structure may have been incorrect. The estimation of realistic variances for the parameter estimates is an area requiring further research.

Acknowledgements

We would like to thank M. Basson, R. Thomson, and two anonymous reviewers for their useful comments on a draft of this manuscript. We also acknowledge the Fisheries Research and Development Corporation for their funding contribution to this project.

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Increase in growth rates of southern bluefin tuna (*Thunnus maccoyii*) over four decades: 1960 to 2000

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Abstract: Estimates of long-term temporal trends and variability in growth are often not available for many commercially exploited fish stocks. An integrated estimation framework that combines growth information from tagging studies, direct age estimates from hard parts, and modal progression estimates from length–frequency data is applied to data on southern bluefin tuna (*Thunnus maccoyii*, SBT) collected over four decades, from 1960 to 2000. By using an integrated approach, a comprehensive set of growth estimates can be obtained for each of these four decades even though substantive deficiencies exist in the coverage of the historical data from any single source. The results confirm previous findings that cohorts from the 1980s grew substantially faster at young ages than cohorts from the 1960s. The results also suggest that the 1970s was a period of transition and that growth of fish up to about age 4 was faster in the 1990s than in the 1980s. The changes in SBT growth over these four decades are consistent with density-dependent responses given the history of exploitation and stock assessment estimates of changes in population size.

Résumé : Chez plusieurs stocks de poissons exploités commercialement, il n'existe souvent aucune estimation des tendances temporelles à long terme, ni de la variabilité de la croissance. Nous ajustons un cadre d'estimation intégrée, qui combine les renseignements sur la croissance provenant des études de marquage, des estimations directes de l'âge basées sur les structures anatomiques dures, ainsi que de l'estimation de la progression des modes d'après les données de longueurs–fréquences, à des données sur le thon rouge du Sud (*Thunnus maccoyii*, SBT) recueillies sur quatre décennies, de 1960 à 2000. L'approche intégrée nous a permis d'obtenir un ensemble complet d'estimations de la croissance pour chacune des quatre décennies, bien qu'il y ait eu des lacunes importantes au cours des années dans toutes les banques de données que nous avons utilisées. Nos résultats confirment les observations faites antérieurement que les cohortes des années 1980 ont crû beaucoup plus rapidement durant leurs premières années de vie que les cohortes des années 1960. Ils indiquent aussi que les années 1970 ont été une période de transition et que la croissance des poissons jusqu'à environ l'âge 4 a été plus rapide durant les années 1990 que durant les années 1980. Les changements dans la croissance du SBT au cours de ces quatre décennies s'accordent bien avec l'existence de réponses dépendantes de la densité, étant donné l'exploitation passée du poisson et les changements dans la taille de la population estimés par évaluation des stock.

[Traduit par la Rédaction]

Introduction

Understanding how growth in fish changes over time can provide important insights into the processes underlying population and ecosystem dynamics (e.g., density-dependent growth and regime shifts in the environment). In addition, estimates of growth rates are fundamental to most stock assessments and to the provision of scientific advice for management decisions. In the absence of any direct information, growth rates are generally assumed to remain static over time in stock assessments. However, if growth rates are changing and these changes are not accounted for, they can result in substantial biases in estimates of stock productivity, sustainable catch levels, and recovery in the case of a depleted stock.

In spite of the importance of knowing how growth may have changed, estimates of long-term temporal trends and variability in growth are seldom available for most commercially exploited fish stocks. Often this is due to the absence of long-term data series. In other cases, a variety of different sources of growth information (e.g., tagging, length–frequency, and direct aging data) may be available, but the data collection processes have resulted in fragmented time series for any single source. When such fragmented data exist, a statistical framework is required that can integrate information from

Received 6 March 2003. Accepted 15 December 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 31 March 2004.
J17382

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 doi: 10.1139/F04-005 © 2004 NRC Canada

the different sources and can also cope with temporal changes in growth. Even the simpler problem of integrating several data sources from a period of static growth is not straightforward. Eveson et al. (2004) have developed an estimation framework that integrates growth data from tagging studies, direct aging of hard parts, and modal length analyses of length–frequency data. In the current paper, we apply this framework to southern bluefin tuna (*Thunnus maccoyii*, SBT) data collected in each of the four decades from 1960 to 2000, and the results are used to quantify changes in SBT growth over this 40-year period.

A large amount of data relevant to the estimation of growth for SBT has been collected since the early 1960s. Several previous studies have used subsets of data from a single source to address the question of changes in SBT growth. Comparisons of growth increment data from tag experiments conducted in the 1960s and 1980s have demonstrated that there was a substantial increase in SBT growth rates between these two periods (Anonymous 1994; Hearn and Polacheck 2003). Concurrently, there was a substantial decline in SBT spawning stock biomass (SSB) and recruitment, suggesting that the change in growth may have been density dependent. It should be noted that changes in growth will confound estimated trends in SSB if not taken into account; however, SBT stock assessments produced since 1993 have incorporated estimated changes in growth. Analyses of length–frequency data for juvenile fish caught in the Australian domestic fishery also demonstrated a substantial increase in the growth of juveniles between the 1960s and 1980s (Leigh and Hearn 2000). Previous studies have been unable to provide estimates of growth rates in the 1970s and 1990s because of the limited data available for these decades at the time of analyses.

Direct aging techniques were developed and verified in the 1990s for aging SBT using their otoliths (Clear et al. 2000). The direct aging data that have accumulated since then provide important growth information on fish born in the 1970s, and they also have the potential to clarify uncertainties that previous studies had in comparing asymptotic lengths (Hearn and Polacheck 2003). Moreover, substantial information on growth of fish spawned in the 1990s is now available. With all of the data currently available and with an integrated analysis method, we were able to obtain rigorous estimates of growth in each of the past four decades and to identify significant changes in growth over this time.

Recent SBT stock assessments suggest that SSB continued to decline from the 1980s until the mid-1990s, after which the trends are uncertain (Kolody and Polacheck 2001; Polacheck and Preece 2001). Given the previously documented changes in SBT growth, the depleted status of the SBT stock, and uncertainty about the most recent stock trends (Polacheck et al. 1999; Anonymous 2001), knowing how SBT growth rates in the 1990s compare with those in previous periods has been seen as an important indicator of the current stock status (Gunn et al. 1998*a*).

The purpose of this paper is to provide reliable estimates of growth for SBT over the past 40 years to improve SBT stock assessments and subsequent management advice. In particular, the estimates should provide a more robust basis for predicting size at age, which is an essential component within the current statistical catch at age assessment models for SBT (e.g., Kolody and Polacheck 2001; Polacheck and Preece 2001) and for predicting consequences of future management actions (e.g., projections, yield per recruit analyses, spawning stock per recruit analyses). The results may provide insights into long-term changes in growth and the possible mechanisms underlying such changes, particularly for large pelagic resources.

Background

SBT is a long-lived, highly mobile, widely distributed fish found throughout most of the southern temperate oceans except in the more easterly regions of the South Pacific (primarily between 35 and 45°S). All information suggests that it is a single stock with only one known breeding area in tropical waters south of Indonesia. Young-of-the-year migrate southward along the west Australia coast (Caton 1991). Juveniles tend to spend their summers (December–April) in southern and eastern coastal waters of Australia where they are harvested by surface fisheries and their winters in deeper temperate oceanic waters where they are harvested by longline fisheries. After about age 5, they are seldom found in nearshore surface waters and are only vulnerable to longline gear. Uncertainty exists about their reproductive biology, but the most recent information suggests that the mean age of maturity is between 10 and 12 years (Gunn et al. 1998*b*; Davis et al. 2001). Once mature, animals migrate between September and April from their temperate feeding grounds to their tropical spawning ground off Indonesia. Individuals can live in excess of 40 years (Kalish et al. 1996).

Commercial fishing for SBT developed in the early 1950s. The Japanese longline fishery, which was initially concentrated on the spawning ground, expanded rapidly. The largest catches of SBT ever taken occurred in 1960 and 1961 (79 371 and 81 605 tonnes, respectively), after which there were substantial declines in both catches and catch rate. In the mid-1960s, the Japanese longline fishery moved away from the spawning ground to the southern feeding grounds where the flesh quality, and hence the price of fish on the Japanese sashimi market, was much higher. The Australian surface fisheries, which began in the 1950s, expanded through the 1970s and early 1980s. A major component of the surface fishery off the southeast coast of Australia collapsed in the early 1980s, which tagging experiments indicate was a period of very high juvenile exploitation rates (Caton 1991). In response, Australia dramatically reduced its catch of juveniles in the surface fishery beginning in 1984, and subsequent international management actions resulted in ~50% catch reduction in the late 1980s. Stock assessments have consistently estimated a continuous decline in SSB from the start of commercial fishing through the mid-1990s but with the rate of decline substantially reduced in the 1990s (Anonymous 2001; Kolody and Polacheck 2001; Polacheck and Preece 2001). The trend since the mid-1990s is uncertain. Estimates of the current SSB relative to the estimated unfished equilibrium SSB range from 4% to 11% (Kolody and Polacheck 2001; Polacheck and Preece 2001).

Materials and methods

Data

Data from three sources were used in the current analyses: (*i*) change in length and time at liberty data from tag–recapture

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experiments; (*ii*) modal length progression within a fishing season from length–frequency data from commercial catches; and (*iii*) direct age estimates from otolith readings combined with the length of the fish at the time of capture. Extensive documentation exists for each of these data sources (see appendix 3 of Polacheck et al. (2003) and references cited therein). We summarize the extent of available data for each source by decade (Table 1).

All tag–recapture data came from fish tagged as juveniles (primarily ages 1–3). Only tagging data from fish tagged and measured at release by trained personnel are used here. Recapture information (particularly recapture length) was obtained from commercial fishers, factory personnel, and scientifically trained staff. Data from trained staff, who are taught a standardized measurement technique, tended to have smaller measurement errors, and hence, these data were assigned a different factor level in the analyses. The maximum time at liberty in the data that we analysed was approximately 14 years; however, the majority of recapture times were less than 4 years. Tagging experiments were conducted during each of the four decades considered, but the number of releases and release years, and hence the extent of growth data, varied considerably. In particular, tagging data from the 1970s are limited, and most tagging occurred in the first half of the decades (Table 1).

Length–frequency distributions of the commercial catches landed in South Australia in each half-month exhibit modes corresponding to age classes. The progression in length of these modes over a fishing season provides information on growth rates. Length samples were taken from landed catches and pooled by half-monthly periods. Caudal fork lengths were measured by trained technicians to the nearest centimetre. The sample length–frequencies from an individual landing were scaled up by the total weight of the landing relative to the weight of the sample to provide an estimate of the length–frequency distribution for an individual landing. The length–frequencies from individual landings were then pooled across half-months to provide an estimate of the length–frequency of the catch for that half-month. Length–frequency data are available since the 1964–1965 fishing season (Table 1). Data after 1989 are not used here because the nature of the surface fishery changed dramatically to one aimed at the sashimi market, in which larger fish within a school are targeted, and later to tuna farming, in which small fish are caught, put live into farms, and fattened up before harvesting. In the former case, there is a potential towards larger, faster growing fish, and in the latter case, very few fish were measured and, moreover, farm fish are not representative of the wild population.

Verified methods for directly aging SBT from otoliths were developed in the 1990s (Clear et al. 2000) and extensive collection of otoliths was undertaken during this period. Otoliths were collected from juvenile fish landed in the surface fishery and from fish caught during tagging programs. Otoliths were also collected by observers aboard Japanese longline vessels operating in the Australian Exclusive Economic Zone as well as on the high seas. In addition, a large number of otoliths were collected at the time of landing in Indonesia from longline vessels operating on the spawning ground. The age range of fish sampled covers 40 age classes, so these data provide information on growth for fish born in each of the four decades under consideration. However, the decadal data

Table 1. Summary of data used in estimation of decadal growth curves for southern bluefin tuna (*Thunnus maccoyii*).

	Otolith readings		Tag–recapture data				Length–frequency data		
					Length range (cm)				
Decade	No. born in decade	Age range (years)[a]	Release years[b]	No. of recaptures	Releases	Recaptures	Sampled years	Mean no. of samples per year (SD)[c]	No. of modes[d]
1960s	277	22–38	1961–1966	791	41–125	60–175	1965–1969	24 019 (6937)	119
1970s	1298	12–30	1973, 1974, 1977, 1978	202	38–78	38–140	1970–1979	21 788 (8903)	288
1980s	668	1–21	1983–1984	2181	40–115	47–173	1980–1989	17 865 (10 875)	269
1990s	281	1–6	1991–1995	2980	41–114	61–183			

[a]All otoliths were collected in the 1990s, so fish born in progressively earlier decades were progressively older by the time of catch.
[b]Years with at least 5% of the total releases for that decade.
[c]Length samples were taken using a two-stage procedure; the sample sizes shown are estimates of the equivalent sample size had a simple random sample been taken (refer to Leigh and Hearn (2000) for details).
[d]A Gaussian mixture model was fitted to the length–frequency data in each half-month and the resulting estimates of length modes and ages were carried forward into the growth model (see Eveson et al. 2004). The total number of modes from all half-months that were carried forward into the growth model are given here.

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sets have a low degree of overlap with respect to ages (Table 1) because almost all otoliths were collected in the 1990s. To avoid aging errors due to uncertainty in the time of band formation, direct aging data were only used for fish collected from October through April (see Polacheck et al. 2003). Also, for fish below age 14, there is evidence that the average size of fish found on the spawning ground is larger than the average size of fish of the same age found off the spawning ground (Farley et al. 2001). Therefore, only the direct aging data for fish aged 14 and older from fish caught on the spawning ground were used to avoid biasing the results for younger ages.

Growth model

The basic growth function used in this paper for describing SBT growth is the von Bertalanffy (VB) log k model described in Laslett et al. (2002). Several studies have found evidence of a significant departure in the growth pattern of SBT from the commonly used VB model (Anonymous 1994; Laslett et al. 2002; Hearn and Polacheck 2003). These analyses suggest that there is a discernible change in the growth process during the transitional period from juveniles to subadults. The VB log k model was developed by Laslett et al. (2002) to accommodate such a transition in growth. It provides a more flexible framework with better statistical properties using the same number of parameters than the two-stage VB growth model used for SBT and similar species (Bayliff et al. 1991; Hearn and Polacheck 2003). The VB log k model uses six parameters to describe length, l, as a function of age, a:

$$(1)\qquad l(a) = L_\infty\left[1 - e^{-k_2(a-a_0)}\left\{\frac{1 + e^{-\beta(a-a_0-\alpha)}}{1 + e^{\alpha\beta}}\right\}^{-(k_2-k_1)/\beta}\right]$$

where a_0 is the theoretical age when a fish would have length zero, L_∞ is the asymptotic length, k_1 is the growth rate parameter for the first stage of growth, k_2 is the growth rate parameter for the second stage of growth, β is a parameter governing the rate of transition between k_1 and k_2, and α is a parameter determining the central age of transition. As age increases, this function makes a smooth transition (according to a logistic function) from a VB curve with growth rate parameter k_1 to a VB curve with growth rate parameter k_2. If $k_1 = k_2$, the model reduces to the standard VB curve.

In addition to this basic model, a seasonal component was included in the model to reflect the fact that SBT growth, particularly as juveniles, appears to be substantially greater during the austral summer months than during the winter (Hearn 1986; Eveson et al. 2004). Seasonality in growth can be modelled by replacing $a - a_0$ with $a - a_0 + S(t)$ in eq. 1, where $S(t)$ is an annually periodic function and t is the fractional time of year since 1 January. We chose to model within-year growth with a sinusoidal function:

$$(2)\qquad S(t) = \frac{u}{2\pi}\sin(2\pi(t - w))$$

where u is the amplitude and w controls the phase shift. Both parameters were estimated in the growth model, with u constrained to be between 0 and 1 to prevent negative growth and w constrained to be between –0.5 and +0.5 (any bounds with a span of 1 could have been chosen due to the periodicity of the function). In this formulation, the rate of growth is maximal at $t = w - 0.5$ and diminishes symmetrically about w to a minimum at $t = w - 0.5$ and $t = w + 0.5$. Other formulations for $S(t)$ could have been considered, but a sinusoidal function appeared to be reasonable based on a visual inspection of the fit, and data limitations did not allow for further resolution of the within-season growth pattern.

Parameter estimation

The model was fit to the data from each of the four decades separately. The tag–recapture data were separated into decades according to the year of release; most tagging events occurred in the first half of each decade, so this made for a natural division. Tagging generally occurs on juvenile fish of ages 1–3, so the "decadal" tag–recapture data sets correspond to fish born during the first half of the decade as well as the last few years of the previous decade. Similarly, the length–frequency data were separated into decades according to the year of capture. Only juvenile fish of ages 1–4 are included from the length–frequency data, so the decadal length–frequency data sets will also include fish born in the last few years of the previous decade (except in the 1960s for which the first year of length–frequency data is 1965). It does not make sense to divide the direct aging data into decades according to year of catch because almost all samples were collected in the 1990s from fish of ages 1–40 (i.e., fish that were born during the 1950s through the 1990s). Instead, the data were separated into decades according to year of birth, as determined from the year of capture and the estimated age. As such, the division of the otolith data is not entirely consistent with that of the other two data sources. This issue is discussed later.

In fitting the model to the data, several sources of variation were taken into account. It is well known that if allowance is not made for individual variability in growth, the resulting estimates can be substantially biased depending on the estimation method (e.g., Maller and deBoer 1988). Individual variability in growth was modelled by allowing asymptotic length to vary from fish to fish. Thus, L_∞ was assumed to be a random normal variable with mean μ_∞ and standard deviation σ_∞. Other formulations for individual variability in growth were considered, but treating L_∞ as a random normal variate both provided an adequate representation of the error and led to similar predictions as other formulations (such as random growth rate parameters). In addition to individual variability in growth, we allowed for additional (confounded) measurement and model error. This was achieved by assuming that there was an additional random normal error associated with every observed length. The mean error was always assumed to be zero; however, the source and magnitude of the variance would be expected to differ among the different data sources and this was taken into account in the estimation model (see Eveson et al. (2004) for details). In total, four different variance parameters for the model/measurement error were estimated: σ_s^2, the variance parameter for the tagging data when the lengths were measured by scientists (this applies to all release lengths and some recapture lengths); σ_f^2, an additional variance component for the tagging data when recapture lengths were measured by fishers; σ_γ^2, the variance parameter for the direct

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aging data; and σ_ε^2, the variance parameter for the length–frequency data.

Parameters were estimated using the integrated maximum likelihood approach presented in Eveson et al. (2004) and Polacheck et al. (2003). Briefly, a separate likelihood function was defined for each data source. Because the data from each source were collected independently of one another (i.e., otoliths were collected from different fish than those that were tagged or sampled for the length–frequency data), the integrated log-likelihood across all of the data sources is simply the sum of the log-likelihood components. The integrated likelihood incorporated common parameters across components for the parameters defining the mean growth function (i.e., μ_∞, k_1, k_2, a_0, α, β, u, and w) and for the asymptotic variance parameter (σ_∞) but had component-specific parameters for the measurement/model error variance terms for each data source. Two additional parameters, $\mu_{\log A}$ and $\sigma_{\log A}$, were estimated in the fitting of the tag–recapture data; they define the lognormal distribution that was used to model the unknown ages at release and are not of primary interest. The choice of distribution for the releases ages will be case specific. For SBT, only juveniles were tagged and rough age estimates based on lengths suggested that a lognormal distribution was appropriate. However, the estimates of the growth rate parameters are generally insensitive to how the distribution of release ages is modelled, as long as a reasonable distribution is used (see Laslett et al. 2002). Overall, the integrated VB log k model has 15 parameters to be estimated.

We also compared the fit of the VB log k model with that of a standard VB growth curve:

$$(3) \qquad l(a) = L_\infty(1 - e^{-k(a-a_0)})$$

where the parameters have the same definition as in eq. 1 above. In this case, we used the same basic likelihood functions and retained the seasonal component. Using a VB curve reduces the number of parameters by three (i.e., β, α, and one of the k parameters are eliminated). Akaike's information criterion (AIC) was used to compare model fits (Akaike 1974).

We computed approximate standard errors for the parameter estimates by first calculating a profile likelihood for each parameter and using it to determine a 95% confidence interval. The profile likelihood for a parameter θ can be calculated by fixing θ and maximizing the log-likelihood over the other parameters and then repeating this procedure for a range of values of θ. To derive a 95% confidence interval (θ_1, θ_2) for θ, draw a horizontal line 1.92 below the maximum likelihood value (the value 1.92 is half of the 95th percentile of a chi-square distribution with 1 df) and determine the values θ_1 and θ_2 where this line intersects the profile likelihood (Cox and Oakes 1994, pp. 34–40). Modern statistical theory suggests that (θ_1, θ_2) is a better 95% confidence interval than common alternatives, such as those derived from the information matrix, score statistics, the Wald statistic, et cetera (e.g., Cox and Oakes 1994). We then calculated a standard error for θ as $(\theta_1 - \theta_2)/3.92$. Strictly, this assumes that the parameter estimators have a normal distribution, resulting in profile likelihoods that are quadratic in shape near the maximum. The vast majority of profiles were nearly quadratic, but we calculated the standard errors using this method even for the occasional skewed profile. We were forced to fix parameters that were on a boundary of the parameter space at their maximum likelihood values; this was true for β in the 1960s and β and σ_γ in the 1970s.

We also estimated standard errors and correlations for the parameter estimates using the observed information matrix. To do this, we generated the log-likelihood $\ell(\theta)$ for various parameter vectors θ near the maximum likelihood estimates $\hat{\theta}$ and fitted the model

$$\ell(\theta) - \ell(\hat{\theta}) \approx -0.5(\theta - \hat{\theta})^T V^{-1}(\theta - \hat{\theta})$$

by quadratic regression, where the unknowns are the elements of the variance–covariance matrix V of the parameter estimators. To ensure that V was positive definite, we were forced to fix β at its maximum likelihood value in all decades. This is a disadvantage over the profile likelihood method, where such a constraint was not necessary for the 1980s and 1990s. For most parameters, the standard error estimates obtained by taking the square root of the diagonal elements of V were similar (to within a few percent) to those obtained from the profile likelihoods; nevertheless, we have more confidence in the standard errors from the profiles and report these in the paper. We do, however, discuss the correlation estimates obtained from the approximate information matrix because calculating joint pairwise profile likelihoods would have been impractical timewise, and the agreement between the standard errors calculated by both methods was excellent.

Results and discussion

Parameter estimates from fitting the integrated VB log k growth model to the decadal data sets suggest that SBT growth has changed over time (Table 2). Although there appears to have been little or no change in the mean asymptotic length (μ_∞), at least since 1970, there has been an increasing trend in growth rates at young ages as reflected in estimates of the k_1 parameters. Comparison of the estimated average growth curves from the maximum likelihood fits indicates that the predicted length of juvenile fish increased between the 1960s and 1980s, with most of the change occurring between the 1970s and 1980s, and changed little between the 1980s and 1990s (Fig. 1). The increase between the 1960s and 1980s is quite substantial, with the estimated average size of a 2-year-old in the 1980s nearly equal to that of a 3-year-old in the 1960s. Although Fig. 1 suggests that there may not be much difference in growth between the 1980s and 1990s, a closer examination of the two curves reveals that a difference of about 4 cm existed at age 2 and of about 2 cm at age 3 (Fig. 2). After this age, the estimated differences were generally less than 1 cm (see below for further discussion of this).

To test formally whether the growth curves estimated for each decade were different, the fit when the data for two adjacent decades were combined was compared with the fits to each decade separately (Table 3). The AIC values for the separate versus combined data indicate that in all cases, there was a statistically significant improvement in the fit (i.e., a lower AIC value) when separate curves were fitted to the data from each decade.

Residuals (observed minus fitted length) were plotted for each data source in each decade (Appendix A, Figs. A1–

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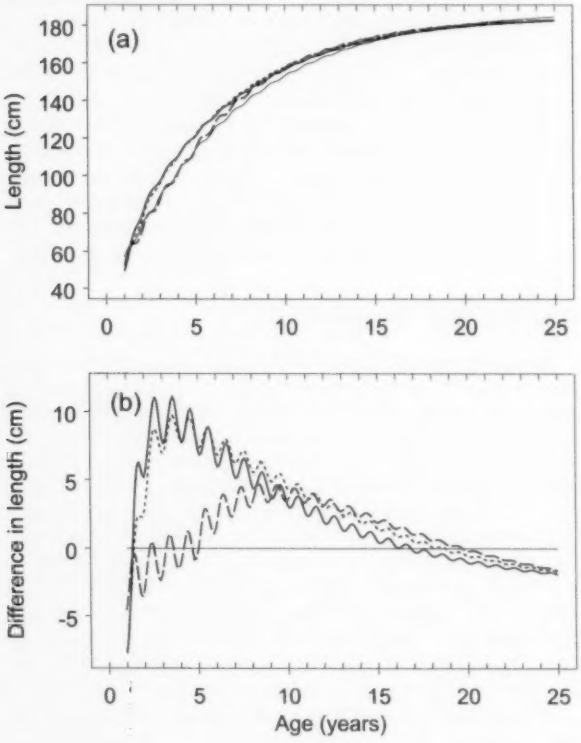
Table 2. Maximum likelihood parameter estimates from fitting the integrated von Bertalanffy log k growth model with a seasonal

Decade	μ_∞	σ_∞	k_1	k_2	a_0	β	a_0	u
1960s	187.8 (0.4)	7.0 (12.4)	0.14 (1.2)	0.15 (3.8)	5.5 (7.4)	30.0[a] (na)	−1.6 (2.6)	0.53 (14.7)
1970s	184.3 (0.3)	7.9 (2.0)	0.15 (1.5)	0.19 (5.0)	5.7 (4.2)	30.0[a] (na)	−1.3 (3.7)	0.92 (11.6)
1980s	184.7 (0.5)	8.1 (4.8)	0.22 (1.3)	0.17 (2.7)	2.8 (3.0)	18.3 (na)	−0.4 (5.5)	0.34 (11.2)
1990s	184.9 (1.7)	8.7 (4.3)	0.25 (3.1)	0.16 (4.4)	2.5 (2.8)	12.4 (na)	−0.3 (11.0)	0.41 (13.1)

Note: Estimates of the coefficient of variation (100 × standard error/|mean|) for the parameter estimates are given in parentheses; na indicates that a for parameter definitions.

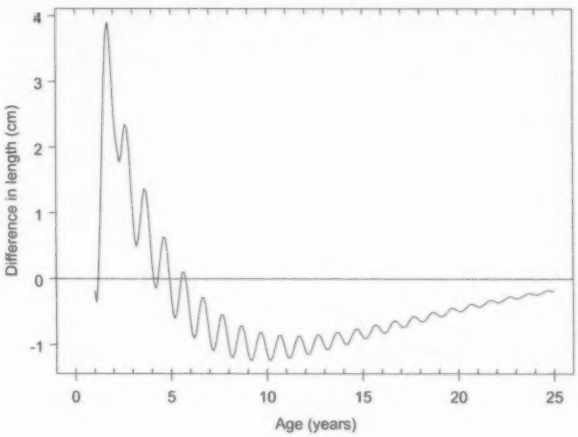
[a]Estimate is equal to the upper or lower bound set for this parameter.

Fig. 1. (*a*) Optimal integrated seasonal von Bertalanffy log k growth curve for each decade for southern bluefin tuna (*Thunnus maccoyii*). (*b*) The same curves plotted relative to the 1960s curve for better comparison. Lower solid line, 1960s; long-dashed line, 1970s; short-dashed line, 1980s; upper solid line, 1990s.



A4). The residuals provide confidence in the integrated model fits and suggest a high level of consistency among the different data sources. The latter is particularly true for the 1980s and 1990s where the data are extensive and there is a large overlap in age ranges among data sources. The only evident concern in the residuals is the lack of fit for the age-1 modal length–frequency data in the 1980s and for the age-1 otolith data in the 1990s. This is explored in detail in Eveson et al. (2004) and Polacheck et al. (2003). This lack of fit appears to stem from the spatial segregation in size and age for 1-year-old fish between Western Australia and South Australia. As a consequence, estimates of growth for fish below age 2 will be sensitive to the relative sampling intensity from these two areas and will contain some ambiguity and uncertainty.

Fig. 2. Optimal integrated seasonal von Bertalanffy log k growth curve for the 1990s plotted relative to the 1980s curve.



Has asymptotic length of SBT changed over time?

Comparison of the parameter estimates for the mean asymptotic length (μ_∞) (Table 2) raises the question of whether μ_∞ has varied over time, in particular whether the decrease in μ_∞ of approximately 3 cm after the 1960s is statistically significant. Fitting all four decades with the constraint of a common μ_∞ parameter resulted in a significant increase in the negative log-likelihood (Table 4, last row) and thus a rejection of the hypothesis of a common μ_∞ (likelihood ratio test statistic = 53 464.5 − 53 456.3 = 8.2, $p = 0.04$ based on a χ^2 distribution with 3 df). The estimates of all parameters other than μ_∞ were virtually unchanged.

Looking at the breakdown of the negative log-likelihood into decades, the increase is driven primarily by the change in μ_∞ for the 1960s, with little difference in the other three decades (Table 4). It should be noted, however, that the profile likelihood for μ_∞ for the 1990s data is quite flat (Fig. 3) and there is little basis for distinguishing whether μ_∞ is different in this decade from that in any of the other decades, including the 1960s. This is not surprising, as the oldest fish in the data sets for the 1990s is around age 10 (by necessity) and fish are still exhibiting substantial growth (i.e., the largest are only ~80% of their asymptotic length). Although the profile likelihood for μ_∞ in the 1980s is steeper and indicates that μ_∞ is significantly different from that in the 1960s (Fig. 3), there are no fish older than age 20 in the 1980s data sets and some indeterminacy might still be expected in the estimate of μ_∞. Thus, the main basis for assessing whether

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component to the data from each decade.

w	$\mu_{\log A}$	$\sigma_{\log A}$	σ_s	σ_f	σ_γ	σ_ε
–0.07 (28.9)	1.2 (1.1)	0.16 (3.1)	2.4 (5.3)	3.1 (9.7)	5.9 (22.9)	2.0 (7.2)
0.06 (29.0)	0.8 (2.2)	0.12 (9.0)	2.1 (26.3)	4.7 (14.4)	0.0[a] (na)	3.5 (4.4)
0.13 (9.2)	0.6 (1.8)	0.17 (1.8)	2.1 (5.5)	4.2 (3.5)	4.6 (7.0)	4.3 (4.7)
0.26 (9.0)	0.7 (2.5)	0.32 (1.7)	1.8 (6.7)	4.9 (3.1)	5.6 (5.9)	

[a]standard error could not be obtained for that parameter. Refer to subsections Growth model and Parameter estimation

Table 3. Comparison of the negative log-likelihood and Akaike's information criterion (AIC) values when a single growth curve is fitted to the pooled data from two consecutive decades compared with when individual growth curves are fitted to data from each decade separately.

	Negative log-likelihood		No. of parameters		AIC value	
Decades compared	Separate	Combined	Separate	Combined	Separate	Combined
1960s and 1970s	12 973.8	13 319.5	30	15	26 007.6	26 669.0
1970s and 1980s	24 169.0	24 565.8	30	15	48 398.0	49 161.6
1980s and 1990s	40 482.6	41 272.9	29[a]	15	81 023.2	82 575.8

[a]There is no length–frequency component, and thus no error variance term, in the 1990s, so the number of parameters is one less for the 1990s than for the other decades.

Table 4. Comparison of the negative log-likelihood values when μ_∞ is estimated separately for each decade (values in Table 2) versus when a common μ_∞ is estimated across all decades (in which case the best fit estimate of μ_∞ is 185.6 cm).

Decade	Separate μ_∞	Common μ_∞
1960s	6 411.9	6 417.3
1970s	6 561.9	6 564.1
1980s	17 607.1	17 607.6
1990s	22 875.4	22 875.5
Subtotal 1970s–1990s	47 044.4	47 047.2
Total	53 456.3	53 464.5

there has been a change in μ_∞ comes from comparing the 1960s and 1970s. In both of these decades, the data include a substantial number of length observations for fish estimated to be over 25 years of age. Based on differences in the negative log-likelihoods from fitting a common μ_∞ to the data from these two decades, the estimates of μ_∞ are significantly different (Table 5) (likelihood ratio statistic = 12 981.1 – 12 973.8 = 7.3, $p = 0.01$ based on a χ^2 distribution with 1 df). Moreover, a non-model-based comparison using a simple t test of the mean lengths of fish estimated to be older than age 25 from the otolith data indicates that the difference in asymptotic length is significant (mean ± SE of 186.0 ± 0.53 cm for the 1960s and 184.0 ± 0.57 cm for the 1970s, $p = 0.01$). In any case, the estimates of length at age for the 1960s are relatively insensitive to the value used for μ_∞ (Fig. 4), and the differences in μ_∞ had little effect on the residual patterns.

Is a VB log k or standard VB model more appropriate?

Comparison of the k_1 and k_2 parameters suggests that they may be equal for the 1960s and perhaps for the 1970s (Table 2), in which case the VB log k model is equivalent to the standard VB growth model. To see if this was the case, the data from each decade were fitted separately to a standard VB model and the resulting fits compared (Table 6). The AIC values suggest that the VB log k model provides a significantly better fit to the 1970s data as well as to the 1980s and 1990s data. However, the AIC values indicate no significant difference between the VB and VB log k models for the 1960s. A comparison of the residuals for the 1960s data sets suggests the same conclusion (compare Figs. A1 and A5 in Appendix A); thus, the parameter estimates from fitting a VB model to the 1960s data are provided (Table 7).

The lack of difference between the VB log k and VB models for the 1960s is not consistent with results in Anonymous (1994) and Hearn and Polacheck (2003). Using only tagging data, these studies found a significant difference for the 1960s between the standard VB model and the two-stage VB model that they were using to model a change in growth rates between juvenile and adult phases (this model is similar to the VB log k model except the transition is abrupt). The reason for the difference appears to be due, at least in part, to the inclusion of the direct aging data in the current study. The direct aging data are highly informative with respect to μ_∞, whereas the tagging data provide only minimal information for estimating μ_∞ (as discussed in Hearn and Polacheck 2003). The direct aging data clearly indicate that μ_∞ is around 186 cm for the 1960s compared with the estimate of 211 cm in Hearn and Polacheck (2003). Reducing the estimate of μ_∞ will increase the estimate of k_2 to achieve a relatively similar fit to the growth information on intermediate ages, since k_2 and μ_∞ are highly negatively correlated. There are other possible reasons for the difference, such as L_∞ was modelled as a random variable in the current paper and the estimation methods used are different.

In any case, the data available for the 1960s may not provide sufficient statistical power to distinguish between the VB and VB log k models. Most of the 1960s growth data

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Table 5. Comparison of the negative log-likelihood values when μ_∞ is estimated separately for the 1960s and 1970s and when a common value is estimated for the two decades (the estimated common value for μ_∞ is 186 cm).

Decade	Separate μ_∞	Common μ_∞
1960s	6 411.9	6 415.5
1970s	6 561.9	6 565.6
Total	12 973.8	12 981.1

Fig. 3. Change in the negative log-likelihood relative to its minimum value as a function of the mean asymptotic length, μ_∞. Solid line, 1960s; long-dashed line, 1970s; short-dashed line, 1980s; shaded line, 1990s.

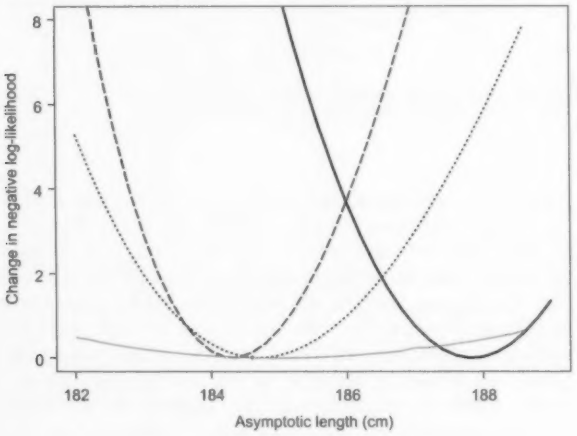
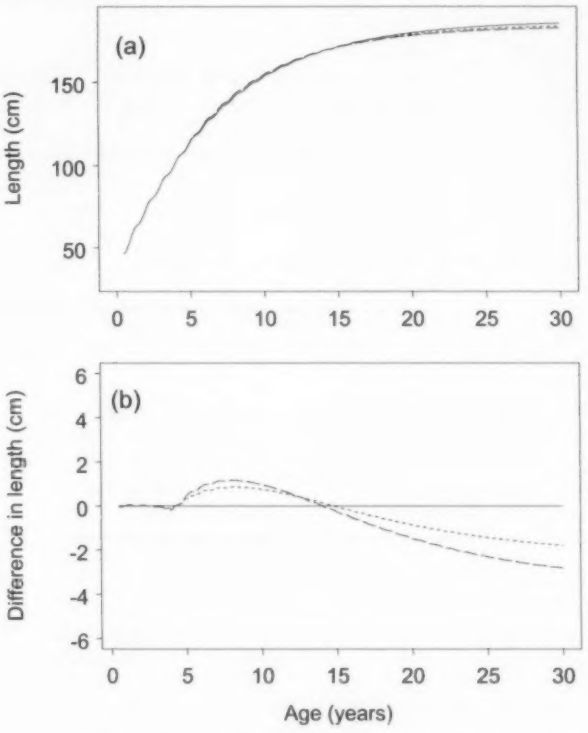


Fig. 4. (*a*) Integrated seasonal von Bertalanffy log k growth curves for the 1960s with μ_∞ fixed at the optimal value for the 1960s data alone (187.8 cm) (solid line), when μ_∞ is constrained to be the same in all decades (185.6 cm) (short-dashed line), and when μ_∞ is constrained to be the same in the 1970s, 1980s, and 1990s (184.4 cm) (long-dashed line). (*b*) The same curves plotted relative to the optimal 1960s curve (i.e., μ_∞ = 187.8 cm) for better comparison.



are for fish either below about age 5 or greater than age 25. The only data in the intermediate age range from 5 to 20 years, which are critical for discerning a transition in growth, come from tag return data in which the return lengths were measured by fishers. The amount of data is small, and there is clearly large measurement error associated with these return lengths, as indicated by the large estimate of the additional variance component for fisher-measured return lengths, σ_f^2 (Table 2).

Can or should the model be simplified?

In addition to considering whether the VB log k model could be simplified to the standard VB model, consideration was also given to whether inclusion of the seasonal component, which required two additional parameters, provided a significantly better fit. In all cases, it did. Furthermore, the estimates of the phase shift, w, indicate that SBT experience their fastest growth around January to March, which is consistent with our understanding that SBT grow fastest during the austral summer.

The estimates of the variability in asymptotic length, σ_∞, across the four decades were similar, ranging from 7.0 to 8.7 cm (Table 2). This was somewhat surprising considering there are no observations for the 1980s and 1990s for older fish that have essentially reached their asymptotic lengths. With the exception of the direct aging variance parameter, σ_γ, in the 1970s, the estimates of the variance parameters for the measurement/model error terms were also relatively similar across the decades. This is encouraging, as it suggests consistency in the growth processes and measurement processes over time and that the model is capturing these reasonably well.

We have not attempted to fit models in which any of the variance parameters were assumed to be common across decades. This was due in part to practical considerations. Attempting to fit models with common parameters proved to be highly computer intensive, requiring extensive amounts of time because of the magnitude of the data sets, the number of parameters that needed to be estimated, and the large number of different parameter combinations that needed to be tested. More importantly, the results of such an exercise would not provide any substantial improvement for modelling growth within a decade or for predicting the expected distribution of lengths at age for these different decades.

Variances/covariances for the parameter estimates

Estimated standard errors for the parameter estimates indicate that most of the parameters are estimated with a high degree of precision (Table 2). In particular, all parameters needed to estimate the expected length at age (i.e., μ_∞, k_1, k_2,

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Table 6. Comparison of the differences in the negative log-likelihood and Akaike's information criterion (AIC) values for the best fit to the standard von Bertalanffy (VB) model and the VB log k model.

	Negative log-likelihood		No. of parameters		AIC value	
Decade	VB	VB log k	VB	VB log k	VB	VB log k
1960s	6 414.9	6 411.9	12	15	12 853.8	12 853.8
1970s	6 575.3	6 561.9	12	15	13 174.6	13 153.8
1980s	17 708.7	17 607.1	12	15	35 441.4	35 244.2
1990s	23 040.9	22 875.4	11	14	46 103.8	45 778.8

Table 7. Maximum likelihood parameter estimates from fitting the integrated von Bertalanffy model with a seasonal growth component to the data from the 1960s.

μ_∞	σ_∞	k	a_0	u	w	$\mu_{\log A}$	$\sigma_{\log A}$	σ_s	σ_f	σ_γ	σ_ε
188.8	7.9	0.14	−1.5	0.49	−0.06	1.2	0.16	2.4	3.0	4.8	2.0
(0.3)	(9.9)	(1.1)	(2.4)	(15.2)	(34.6)	(0.9)	(3.1)	(5.4)	(20.6)	(32.5)	(7.0)

Note: Estimates of the coefficient of variation (100 × standard error/|mean|) for the parameter estimates are given in parentheses.

a_0, α, β, u, and w) have a coefficient of variation less than 11%, and generally much smaller, except for u and w. These latter two parameters determine the seasonal pattern of growth, and it is not surprising that they are estimated less precisely because the amount of information on the seasonal component is substantially less (e.g., only from the short-term tag returns and the within-year pattern of the means in the length–frequency distributions over a limited portion of the year). Moreover, there appears to be some year-to-year variation in the period of peak growth within the austral summer months. This would be expected given annual variation in environmental conditions. Nevertheless, even for u and w, the estimates of the coefficients of variation are less than 30%.

It should be noted that we were unable to estimate a standard error for β, which is the parameter governing the rate of transition between the two growth phases. In all decades, β was estimated to be large (>12 and frequently equal to the preset upper bound of 30), and its profile likelihood was steep up until a value of about 10, beyond which it was very flat. For a VB log k growth curve, any value of β over about 10 suggests a very quick transition between the two phases of growth; thus, even though the exact value of β is difficult to estimate precisely, the model is still predicting with a high degree of certainty that the transition between k_1 and k_2 is very sharp. The fact that we were unable to estimate a standard error for β reflects the fact that there is basically no predictive or practical difference in the value chosen for β once it is estimated to be large (e.g., >10).

We found some of the parameter estimates to be highly correlated, mostly negatively (e.g., Table 8). Most of these are expected given the structural form of the model. Negative correlations between the asymptotic length and growth rate parameters are a well-known feature of VB-type growth models and mean that simple comparisons of individual parameter estimates can be misleading as an indicator of changes in growth when the data come from a restricted portion of the age range. One of the strengths of the integrated approach used here is that it ensured that data over a wide range of ages were incorporated into the estimates. As a result, the parameter estimates and the estimates of length at age are highly robust and allow for a reliable comparison between decades. A few of the variance-related parameters are also highly negatively correlated. This is not surprising, as they are providing alternative ways of explaining the residuals around the mean growth curve (e.g., increasing the value of one results in less variance that needs to be explained by the others).

The estimates of the variance–covariance matrix can be used to produce estimates of the confidence intervals around the predicted growth curves based on normality assumptions. We calculated these confidence intervals and found that they are very narrow. The upper and lower 95% confidence intervals are almost indistinguishable from the predicted curves when plotted on the same scale as in Fig. 1. Such narrow confidence intervals suggest that the mean growth curve is being estimated with a high degree of precision. It is important to note that they do not reflect the amount of individual variation in growth around the mean curve, which we know to be large (as indicated by the variance-related parameter estimates).

The estimates of the standard errors and respective confidence intervals are smaller than we expected. In part, this reflects the large amount of data contributing to the estimates, the consistency across different data sets, and the allowance for individual variation in growth. On the other hand, there are a number of reasons why the uncertainty may be underrepresented: (*i*) model uncertainty (e.g., the choice of modelling L_∞ as a random effect), (*ii*) lack of normality in the parameter estimates, (*iii*) nonindependence in the data (e.g., nonindependence among fish tagged in the same school, overestimation of the effective sample size in the length–frequency data, reader biases in the otolith data, etc.), (*iv*) nonrepresentative sampling from the SBT population (e.g., all tagging was done in nearshore surface fisheries close to Australia, potential size selectivity in the catch, etc.), and (*v*) the tag–recapture model fitting procedure is very flexible and may overfit the data with respect to the age at release (Polacheck et al. 2003).

Division of data sets into decades

Our results provide evidence that SBT growth has changed over time. We acknowledge that there is no reason for growth

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Table 8. Example of the estimated correlation matrix for the parameter estimates from the von Bertalanffy log k model fit.

	μ_∞	σ_∞	k_1	k_2	α	a_0	u	w	$\mu_{\log A}$	$\sigma_{\log A}$	σ_s	σ_f	σ_γ	σ_ε
μ_∞	1.00	0.07	**–0.56**	**–0.82**	**0.40**	–0.15	0.15	0.16	0.22	0.08	0.07	0.03	0.15	0.13
Σ_∞		1.00	0.30	–0.10	–0.27	0.31	0.01	–0.02	**–0.36**	–0.18	**–0.36**	–0.19	**–0.50**	0.15
k_1			1.00	**0.50**	**–0.83**	**0.81**	–0.13	–0.19	–0.88	–0.10	–0.20	–0.21	–0.23	0.23
k_2				1.00	**–0.58**	0.19	–0.12	–0.18	–0.23	–0.06	–0.06	–0.01	–0.13	–0.11
α					1.00	**–0.68**	0.09	0.20	**0.77**	0.08	0.28	0.06	0.23	–0.13
a_0						1.00	–0.07	–0.24	**–0.84**	–0.05	–0.15	–0.24	–0.14	0.33
u							1.00	0.00	0.14	0.07	–0.08	0.00	0.08	–0.01
w								1.00	0.23	–0.14	0.03	0.11	0.02	0.00
$\mu_{\log A}$									1.00	0.06	0.21	0.21	0.19	–0.31
$\sigma_{\log A}$										1.00	–0.06	0.08	0.12	–0.02
σ_s											1.00	**–0.43**	0.20	–0.01
σ_f												1.00	0.09	–0.14
σ_γ													1.00	–0.01
σ_ε														1.00

Note: Shown here are the results for the 1980s data. The results for the other decades were qualitatively similar (see Polacheck et al. 2003). Correlations greater than 0.35 in magnitude are in bold.

changes to conform to decades, and ideally, we would like a growth model that allows for time-varying growth parameters. We have attempted, with some success, to fit a simple VB model with a time-varying k parameter to all years' data (1960–2000) using only one data source at a time (see appendix 8 of Polacheck et al. 2003); however, attempts to expand the analysis to integrate across data sets or to use the VB log k model instead of the simple VB model proved unfeasible and is an important area for further research.

In the absence of an adequate time-varying growth model, we needed to group the data to get sufficient information for estimating the model parameters reliably. Preliminary investigative analyses of the tagging data (such as using a simple VB equation and a fixed value of L_∞ to calculate k for each fish, or fitting an experimental time-varying VB model as described above) suggested that the growth rate was relatively stable between 1960 and 1970, and again after 1980 (although at a higher rate), and that the 1970s was a transitional period of unstable growth. As such, the choice to divide the data according to decades seemed reasonable provided some caution is taken when interpreting the results for the 1970s.

As discussed previously, the division of the otolith data into decades was not entirely consistent with the other two data sources. We considered an alternative partitioning into decades, which attempted to better align the three data sets. In particular, the otolith data were divided such that the data for a given decade excluded fish born in the last 2 years of the decade and included fish estimated to have been born in the last 2 years of the previous decade. Furthermore, the last year of length–frequency data from each decade was excluded to avoid any ambiguity as to which decade the data should belong to (since fish caught in that year would have been born during the last several years of the decade, not just the last 2 years). The parameter estimates from fitting the VB log k model to these alternative decadal data sets were almost identical to those in Table 2 for the 1960s, 1980s, and 1990s. The only notable differences were for the 1970s, with parameter estimates for the mean growth curve becoming μ_∞ = 187.9, k_1 = 0.17, k_2 = 0.14, α = 2.5, and β = 30. Furthermore, with the new data divisions, the VB log k model provided only a marginally better fit than the simple VB model in the 1970s (AIC value of 11 955.3 for the VB log k model compared with 11 957.9 for the VB model). The sensitivity of the 1970s results to relatively small changes in the data supports the hypothesis of the 1970s being a phase of unstable, transitional growth.

General discussion

The estimation of fish growth is challenging and complex, particularly for long-lived species such as SBT for which growth processes can be expected to vary in different components of the life cycle and can change over time, potentially differentially with age. This necessitates extensive data collection over considerable time periods if reliable estimates are to be obtained. Moreover, given the long life span of SBT, commonly used sources of information on growth (e.g., length–frequency and tagging data) are likely to be informative for only portions of the age range. As such, it is important to have methods that can incorporate and integrate a variety of data sources.

The estimation approach used here to integrate across different data sources provided a comprehensive set of estimates for SBT growth over four decades. Substantive deficiencies exist in the historical data from any single source, and for the 1970s, none of the individual data sources by themselves were sufficient to provide reliable estimates of growth. Combining length–frequency, tag–recapture, and direct aging data produced a comprehensive and long-term data set and proved to be a powerful means of obtaining estimates for the 1960s and 1970s periods. Nevertheless, limitations still exist in the coverage provided by this integrated data set that need to be taken into account in interpreting the results. In general, the direct aging data provided the best information on asymptotic length, the length–frequency data the best infor-

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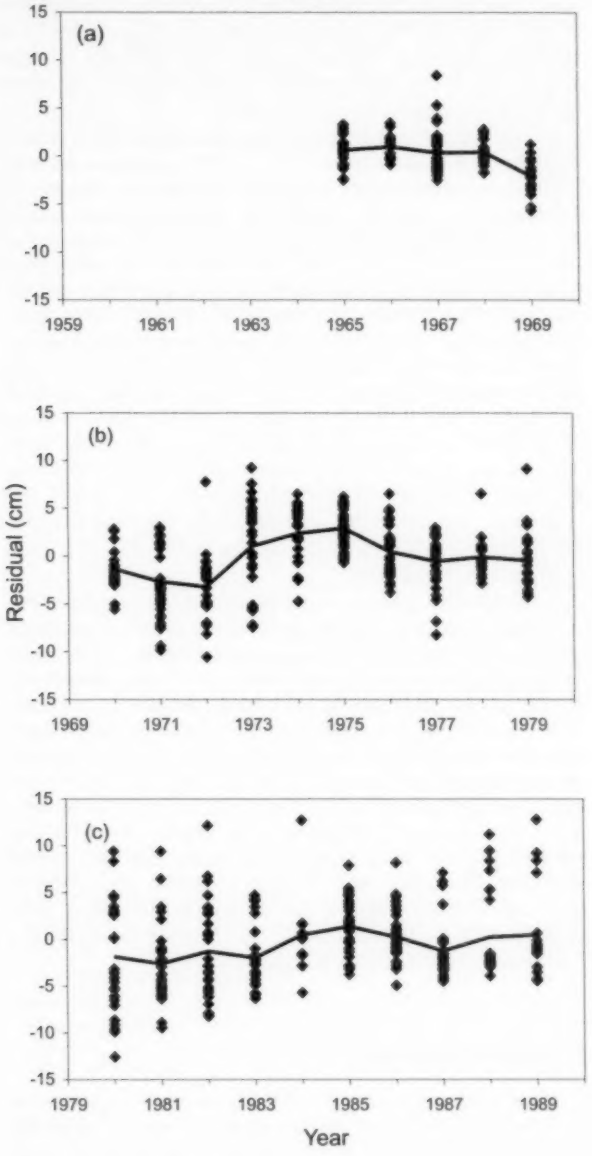

Fig. 5. Residuals (observed minus fitted) for the length–frequency data as a function of year for the best fit to the von Bertalanffy log k model for the (*a*) 1960s, (*b*) 1970s, and (*c*) 1980s.

mation on within-season growth, and the tag–recapture data the best information on growth at intermediate ages and on between-fish variability (σ_∞).

The results from applying the integrated model to the data from the 1960s and 1980s confirm previous results that the latter cohorts grew substantially faster at younger ages. This difference was seen in three independently derived data sources, indicating that the observed difference is not an artefact of differences in the data collection or processing procedures over time. The estimated difference in the growth curves between these two decades is somewhat less than that estimated in either Anonymous (1994) or Hearn and Polacheck (2003). These previous studies were based only on tag–recapture data and used Fabens' (1965) estimation method without any allowance for individual variability in growth. The additional information gained from the other data sources, especially on asymptotic length, appears to be the primary reason for the difference. Furthermore, Fabens' (1965) approach has been shown to be biased if there is individual variability in L_∞ (Maller and deBoer 1988), which the results presented here strongly suggest there is. Thus, taking into account this variability could also account for some of the difference.

The results indicate that growth of young fish was faster in the 1990s than in the 1980s up to about age 4. The estimated growth curve suggests that after this age, growth slowed down so that fish from the 1990s are predicted to be the same size on average as those born in the 1980s. However, the limitations in the 1990s data need to be recognized. Only cohorts born before 1995 can possibly contribute data on growth for fish older than age 5 because 2000 was the last year for which data were available for inclusion in this study. As such, the estimated growth curve for the 1990s past age 5 is based exclusively on growth experienced in the first half of the decade. Thus, if growth rates were on average increasing in the 1990s, the estimates for the older ages may be biased downward relative to what may be observed when more complete and representative data are available. In this regard, it is worth noting that in the tag–recapture data, there is a small tendency for the residuals for the oldest fish from the 1990s to be negative. These fish were born in the first few years of the 1990s or in some cases in the late 1980s.

The 1970s results in Table 2 suggest that fish growth was slower in the first life stage than in the second (i.e., $k_1 < k_2$). This is the reverse of the situation for the 1980s and 1990s and contrary to what was expected given previous discussions and suggestions for why a transition may occur in SBT growth (e.g., Hearn and Polacheck 2003); however, as seen in the section Division of data sets into decades, the 1970s results were sensitive to which data were included. The 1970s appear to have been a period of transition with quite variable growth. Examination of residual plots for the length–frequency data by year (Fig. 5) strongly suggests that growth in the first few years of the 1970s was slower than in latter years. Thus, when the data are pooled for this decade, they will provide intermediate values. Attempts to further resolve the growth in the 1970s using this integrated framework were not successful. The data for the 1970s are relatively sparse and did not, for example, support half-decadal estimates. The limitations in the 1970s data are important to recognize in any interpretation of the results. In particular, there is little information on growth for intermediate ages (i.e., between ages 4 and 15).

It is important to consider what the estimates of the growth parameters represent when interpreting them. At a fundamental level, the estimated growth model provides a mathematical description of the realized average length at age, along with associated variances in the distribution of length at age, for the group of fish over which the data have been aggregated. The results do not provide a direct description of the growth at any particular instant in time but rather an average

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across decadal time periods. Different components/ages within the population at any given instance may have been following very different growth trajectories depending on the cumulative factors that have affected, and are affecting, their growth.

At another level, the estimated growth parameters provide insight into the underlying growth processes, how they have changed, and the factors responsible for them. However, caution is warranted because of the problem of inferring process from pattern and the potential problems with the lack of separability in the observed realization of multiple and cumulative effects. For example, observed growth comes from individuals that survived to that age. To the extent that there is size-specific mortality within an age group (either natural or fishery induced), the resulting observed growth curves represent a combination of the underlying growth and mortality processes.

All of the observed data on growth come from fish that were captured in a fishery (in most cases commercial but some "scientific" in the case of tagging). If there is large size selectivity in fishing within an age class, then the resulting growth curves do not provide fully unbiased estimates for the underlying population. In terms of predicting the age distribution of the catch within a statistical catch at age assessment, this would not be a problem. Nevertheless, potential size selectivity is an inherent limitation of using fishery-collected data to study growth. We ensured that any known sources of potential bias were taken care of in our analyses. Any remaining biases would have had to change substantially over time to have created the observed differences in the estimated growth rates. As pointed out by one reviewer, if size selectivity on larger fish has increased over time, this would provide a possible explanation for the observed changes in growth. Although this hypothesis cannot be addressed statistically, we do not consider it to be very plausible given the nature and history of the SBT fishery. First, changes in growth were evident in both the longline- and surface-caught fish and these two gear types have very different selectivity characteristics; therefore, it seems unlikely that selectivity biases were substantial (particularly considering the wide range of size and age classes caught by longline gear). Second, although the major change in growth coincided with increased and intense fishing pressure on juveniles by surface fisheries in Australia, the market for these fish at that time (before the mid-1980s) was solely for canning, for which no large incentive to target larger fish existed. Also, purse seining, which was the principal gear employed in South Australia, does not allow for size selection within a school, and schools generally contain fish from a wide range of sizes. In addition, the intensity of fishing pressure combined with the scarcity of fish in the Great Australian Bight during the 1980s resulted in strong competition among vessels and any school detected was likely to be set upon. Finally, if intense selection pressure for the faster growing fish was occurring in the juvenile fishery, then those that escaped should have been the slower growing, smaller individuals from a cohort; however, the older fish subsequently caught in the longline fishery were also larger at a given age than in the past. Because longline fisheries catch a very broad range of sizes, it seems unlikely that they could consistently catch only the larger sized fish of a cohort, particularly given the overlap in size among adjacent age classes past about age 5. Also, longline gear and fishing practice are considered to have been relatively unchanged over time. Finally, the magnitude of the change in length for 3- and 4-year-old fish appears too great to be explained by a selection effect (e.g., a large fraction of the direct-age juvenile fish caught in the 1980s are outside the expected size range of fish for a similar age in the 1960s).

As an alternative hypothesis, the changes in SBT growth over the four decades from 1960 to 2000 are consistent with a density-dependent response to changes in juvenile abundances. During this 40-year period, SBT recruitment is estimated to have substantially declined; stock assessments suggest that on average, recruitment was ~20% lower in the 1970s than in the 1960s and was also ~60% lower in the 1980s and the first half of the 1990s than in the 1960s (Caton 1991; Kolody and Polacheck 2001; Polacheck and Preece 2001). Furthermore, the late 1970s and early 1980s were periods of very high juvenile SBT exploitation. These declines in both recruitment and juvenile abundance would have reduced competition for resources among juvenile fish, and as such, the increase in the juvenile growth rate (k_1) in the 1980s may represent a density-dependent response. The small but continued increase in the juvenile growth rate estimated for the 1990s is consistent with the continuing but slowed declines estimated in recruitment.

Although this density-dependent hypothesis is speculative, it is broadly consistent and plausible given the set of estimated growth rate parameters from this integrated analysis, the history of the fishery, and the general trends in SBT stock abundance. If changes in SBT growth are density dependent, it seems probable that they are driven primarily by decreased competition for resources among young (1- to 3-year-old) fish, not only because this is the age range that exhibited the greatest increase in growth rates but also because fish at these ages are found aggregated in nearshore Australian waters during summer (the season of most rapid growth) and may also be segregated from the older population during winter (based on longline catch data). If this hypothesis is correct, then juvenile SBT growth rates would be expected to decline if a substantive increase in recruitment occurred.

Acknowledgments

We wish to acknowledge and thank the very large number of individuals who, over the last 40 plus years, collected the biological samples and data that underpin all of the analyses in this paper. We also thank the SBT fishing industry for their cooperation and help over this same time with various aspects of the sampling, data collection, and tagging programs. We are grateful to Naomi Clear and Jessica Farley for their assistance in the provision and interpretation of the otolith data and Bill Hearn for his help with the location and interpretation of the historical tagging and length–frequency data. Finally, we wish to thank Alistair Hobday and Jeffrey Dambacher, as well as two anonymous reviewers, for their valuable comments on a draft manuscript. The Australian Fisheries Research and Development Corporation provided funding support for this project.

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Appendix A. Residual plots

Residual plots (Figs. A1–A5) appear on the following pages. The estimator of the age at release, $\widetilde{A}_f$, is described in Laslett et al. (2004).

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Fig. A1. Residual plots for the integrated von Bertalanffy log k model with a seasonal component fitted to the 1960s data sets for southern bluefin tuna (*Thunnus maccoyii*): residual lengths (observed minus fitted) for the (*a*) direct aging data, (*b*) length–frequency data, (*c*) tagging release data, and (*d*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns.

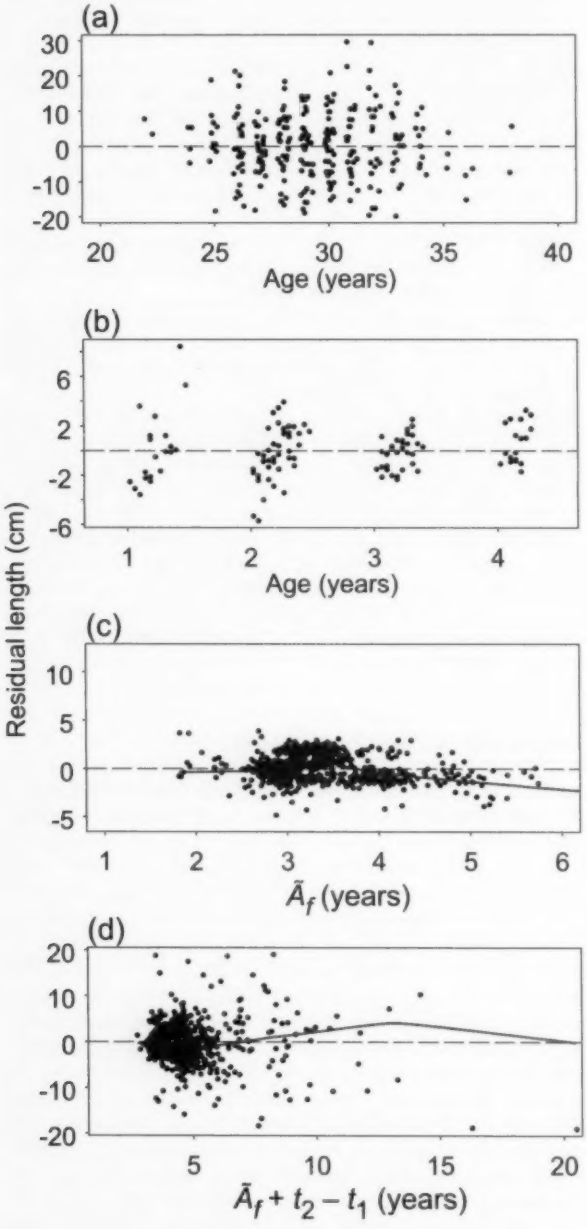

Fig. A2. Residual plots for the integrated von Bertalanffy log k model with a seasonal component fitted to the 1970s data sets: residual lengths (observed minus fitted) for the (*a*) direct aging data, (*b*) length–frequency data, (*c*) tagging release data, and (*d*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns.

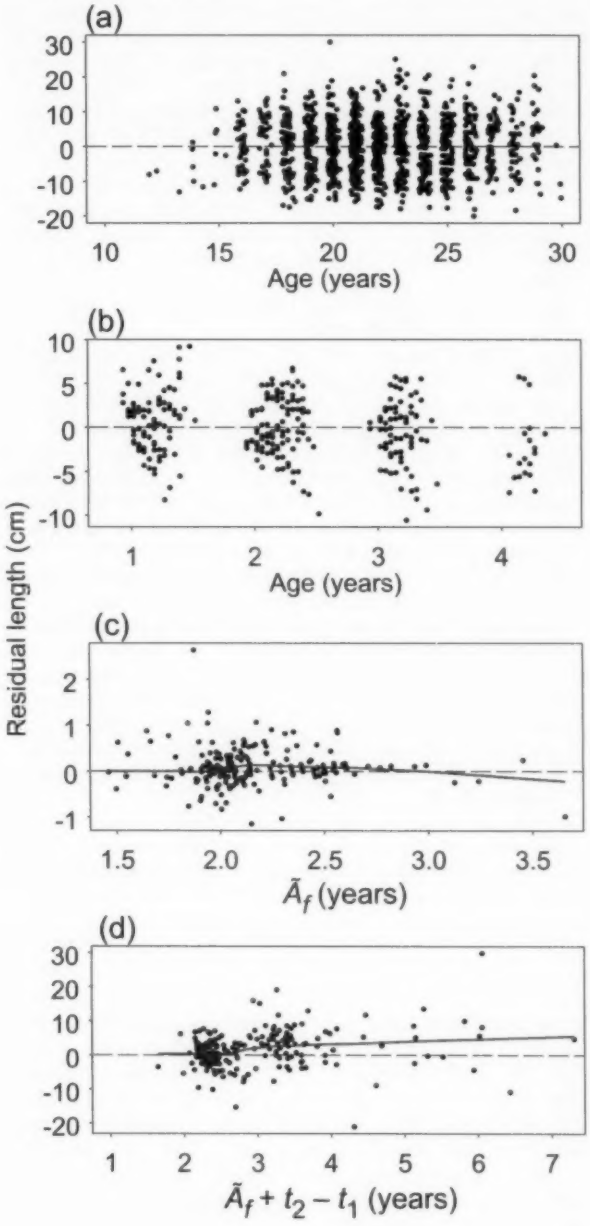

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Fig. A3. Residual plots for the integrated von Bertalanffy log k model with a seasonal component fitted to the 1980s data sets: residual lengths (observed minus fitted) for the (*a*) direct aging data, (*b*) length–frequency data, (*c*) tagging release data, and (*d*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns.

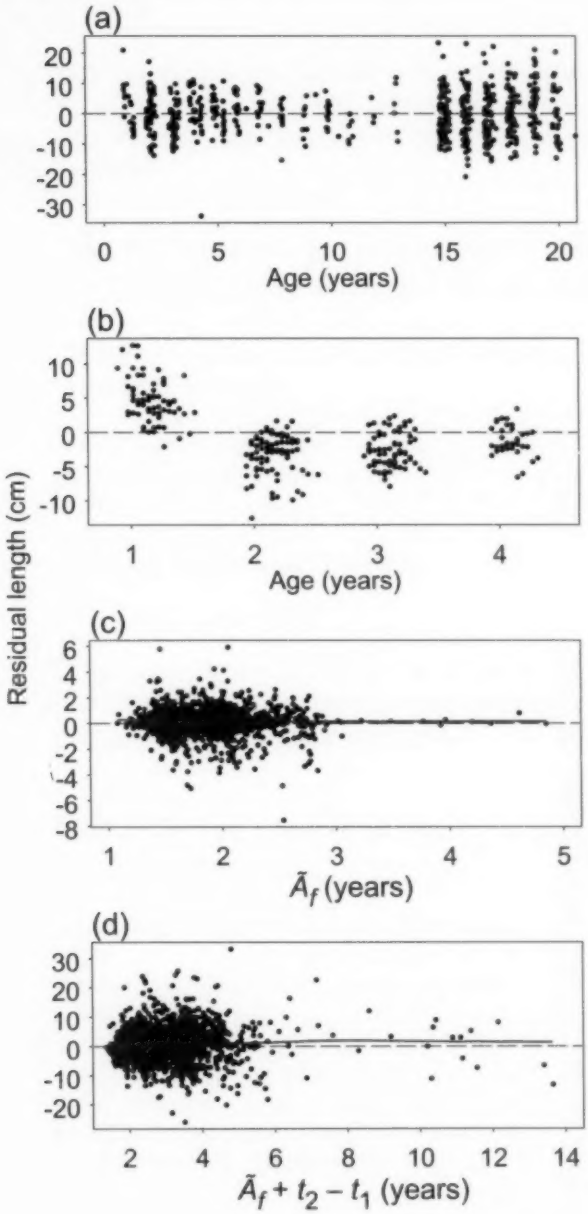

Fig. A4. Residual plots for the integrated von Bertalanffy log k model with a seasonal component fitted to the 1990s data sets: residual lengths (observed minus fitted) for the (*a*) direct aging data, (*b*) tagging release data, and (*c*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns. (Recall that no length–frequency data were included in the growth model for the 1990s.)

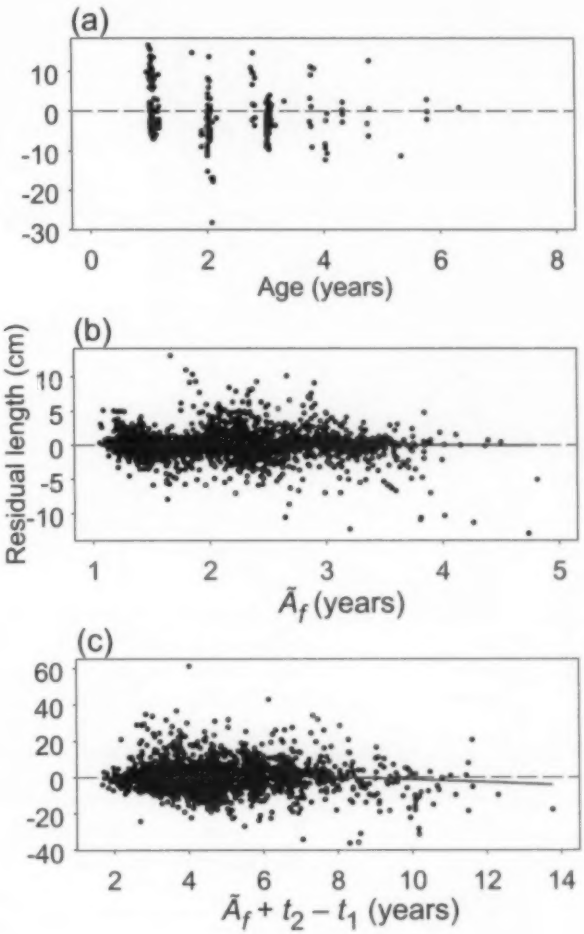

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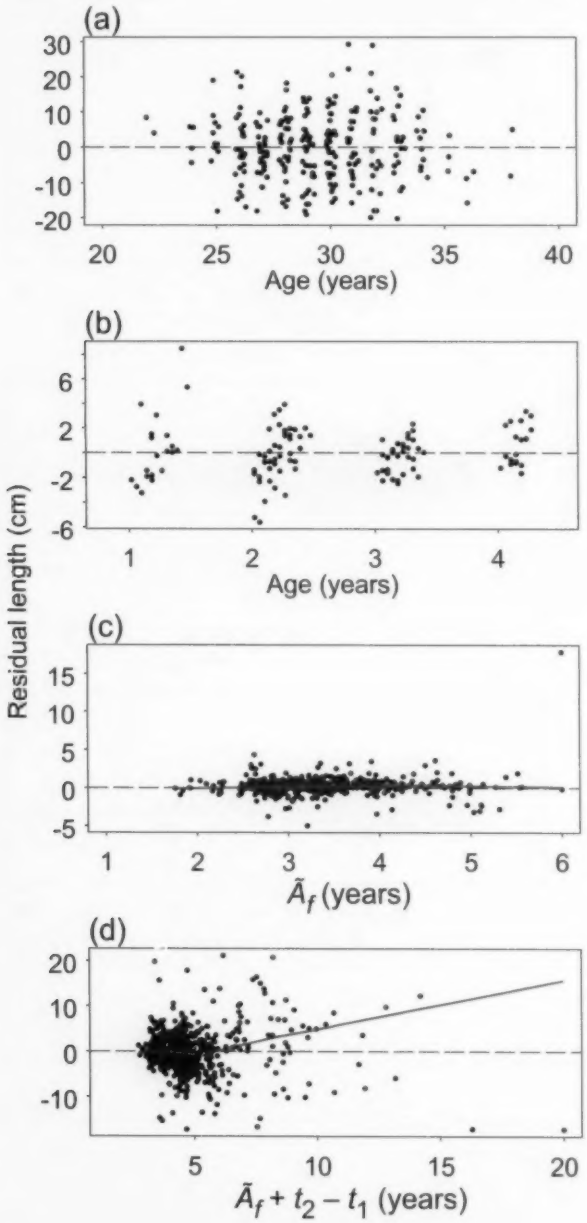
Fig. A5. Residual plots for the integrated von Bertalanffy model with a seasonal component fitted to the 1960s data sets: residual lengths (observed minus fitted) for the (*a*) direct aging data, (*b*) length–frequency data, (*c*) tagging release data, and (*d*) tagging recapture data. The release length residuals are plotted against $\tilde{A}_f$ (the estimated age at release relative to a_0), and the recapture length residuals are plotted against $\tilde{A}_f + t_2 - t_1$ (the estimated age of recapture relative to a_0). A local linear smooth has been put through the release and recapture residuals to help reveal any patterns.



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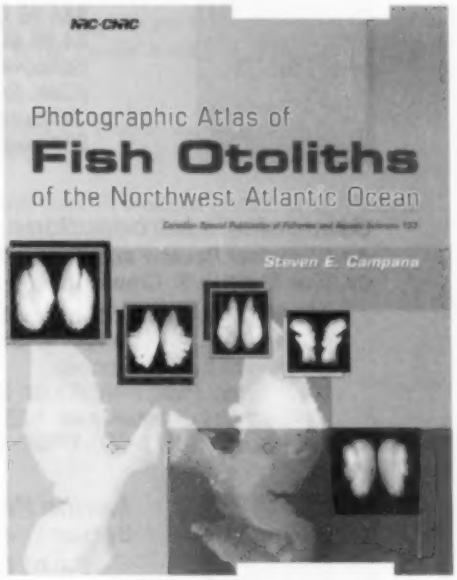

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Printed in Canada by / Imprimé au Canada par
NRC Reprographic Services / Service de reprographie CNRC
Page production by / Mise en page par
NRC Research Press / Presses scientifiques du CNRC

0706-652X(200402)61:2;1-J